A Monograph of the Tape-worms of the Sub-family Avitellininæ, being a Revision of the Genus Stilesia, and an Account of the Histology of Avitellina centripunctata (Riv.).

By

Lewis Henry Gough, Ph.D.,

From the Zoological Laboratories of the Universities of Basel, Switzerland, and of Leeds, England.

With Plates 12–14 and 6 Text-figures.

The following paper was commenced at Leeds; it was originally intended only to give an account of the anatomy of Stilesia hepatica, Wolffhügel, which has been very imperfectly known until now, as much of the original description is not only incorrect but actually misleading. That section of this paper treating of Stilesia hepatica, Wolffhügel, was prepared at Leeds. I am much indebted to Prof. Garstang for his hospitality in placing his laboratory at my disposal and for the encouragement I received from him, and desire to express my thanks to him for it here.

As I was spending the winter at Basel, Switzerland, Prof. Zschokke kindly offered me a table in his laboratory, and suggested extending the scope of the paper I had commenced at Leeds so as to cover all the known species of the genus Stilesia; he also helped me to bring together the material required in order to make the paper complete. Its scope was again extended to include an account of the histology of Avitellina (Tænia) centripunctata (Riv.), on account of several histological peculiarities of the worm, which seem to throw a new light on the problems connected

with the structure of the Cestodes, and because my material was in a much better state of preservation than is usually seen. Excepting the account of the histology and anatomy of Stilesia hepatica, Wolffhügel, the rest of this paper has been prepared at Basel.

I feel great pleasure in expressing my thanks to Prof. Zschokke for his hospitality and assistance.

My thanks are also due to Prof. Railliet, of Alfort, who placed not only the original material of Stilesia vittata, Railliet, at my disposal, but also more recent specimens of both that species and of Stilesia globipunctata (Rivolta). I must also thank Prof. Colin, of the Natural History Museum of Berlin, for the loan of the type-specimens of Stilesia hepatica, Wolffhügel, and Prof. Fuhrmann, of Neuchâtel, for having kindly re-examined his specimens of Stilesia sjöstedti at my request and for the loan of his type-specimens, thus enabling me to fix its true systematic position, and for procuring material of Dibothriocephalus and Triænophorus for me.

To my friend Dr. O. Huber I am indebted for the delineation of figs. 5, 6, 7, and 12, and desire to express my thanks to him here.

I have divided this paper into two chapters. The first deals with the systematic revision of the genus Stilesia; the second is an account of the histology of Avitellina centripunctata (Riv.).

Revision of the Genus Stilesia, Railliet.

The material employed in connection with this revision of the genus is derived from the following sources:

Stilesia globipunctata (Rivolta).

(1) From the small intestine of a goat, collected in British India by Leese, from Prof. Railliet's collection (No. P196[3]).

(2) From the small intestine of a sheep, collected in France, from Prof. Railliet's collection (No. P191).

Stilesia vittata, Railliet.

(1) From the small intestines of a dromedary, collected at Alfort, April 22nd, 1896, from Prof. Railliet's collection (No. P196). Type.

(2) From the small intestines of a dromedary, collected at Alfort, May 27th, 1906, from Prof. Railliet's collection (No. P192).

(3) From the small intestine of a dromedary, collected in British India by Leese, 1909, from Prof. Railliet's collection (No. P713[50]).

Stilesia hepatica, Wolffhügel.

(1) From the bile-ducts of sheep and goats, collected in German East Africa, belonging to the Natural History Museum, Berlin. Type.

(2) From the bile-ducts of sheep, collected in the Lydenburg District, Transvaal, belonging to the Natural History Museum, Berlin. Co-type.

(3) From the bile-ducts of sheep, collected at Pretoria, Transvaal, 1909 (author's collection).

Stilesia Sjöstedti, Fuhrmann.

(1) From the bile-ducts of Hippotragus equinus, collected in North-east Rhodesia (author's collection).

(2) From Tragelaphus silvaticus mernensis, collected by the Sjöstedt expedition (Fuhrmann's type).

Avitellina centripunctata (Rivolta).

(1) From the small intestines of sheep, collected at Pretoria, Transvaal, 1909 (author's collection).

History of the Genus Stilesia.

The genus Stilesia was proposed by Railliet (1893) to include two species of tape-worm from the small intestines of sheep, which had been described by Rivolta in 1874 as Tænia globipunctata and Tænia centripunctata.

The best description of these two species available hitherto was by Stiles (1893), who also revised the generic diagnosis, basing his revision on the then known data, though evidently not feeling quite sure as to the desirability of leaving both species in one genus.

In 1896 Railliet described a new species, Stilesia vittata, from the intestines of a dromedary; he considered this species to be very closely allied to Stilesia globipunctata (Riv.), and, perhaps, only to be a variety.

In 1903 another new species, closely related to Stilesia globipunctata (Riv.), was described by Wolffhügel, from the bile-ducts of sheep and goats in South and East Africa, as Stilesia hepatica.

In 1906 Tempère briefly refers to Stilesia centripunctata and figures its scolex, apparently only quoting from Railliet (1893) and Neumann (1893).

In 1908 Gough states briefly that Stilesia hepatica, Wolffhügel, is usually not double-pored.

In 1909 Fuhrmann places Stilesia and Thysanosoma in a new sub-family, the Thysanosominæ.

In 1909 Fuhrmann describes a new species from Tragelaphus sylvaticus mernensis, collected by Dr. Sjöstedt on the Masai steppes, as Stilesia sjöstedti.

In 1909 Gough gives a full description of the anatomy of Stilesia centripunctata (Rivolta), with remarks on Stilesia hepatica, Wolffhügel.

At present, therefore, the genus contains the following five species:

Stilesia centripunctata (Rivolta), 1874; Stilesia globipunctata (Rivolta), 1874; Stilesia vittata, Railliet, 1896; Stilesia hepatica, Wolffhügel, 1903; Stilesia sjöstedti, Fuhrmann, 1909.

The last four species agree very closely in their anatomy; the first differs from all the others in several important respects of generic value. A new genus will therefore have to be proposed for Stilesia centripunctata.

Stilesia globipunctata (Riv). is the type species of the

genus Stilesia; this species and Stilesia vittata, Railliet, were described as having irregularly alternating genital pores. Stilesia hepatica, Wolffhügel, and Stilesia sjöstedti, Fuhrmann, have been described as double-pored; they do not, however, differ from the type species in this respect, all four being without doubt single-pored.

The generic diagnosis, as revised by Stiles (1893), reads:

"Stilesia, Railliet, 1893. Type species, S. globipunctata (Riv.), Railliet, 1893. Head with four suckers, but no hooks. Strobila thin and narrow. Genital pores irregularly alternate. Segments broader than long. Two distinct sets of testicles present in each segment, one on each side, but no testicles in the median line. Eggs very small and with but one shell.

"The following points, which may prove to be of generic value, have been established only for S. globipunctata: Genital canals pass dorsally of nerve and ventral canal, but ventrally of dorsal canal. Egg-shell with two conical projections at opposite poles.

"Habitat: Intestine of sheep. Development unknown."

The generic description can now be amplified to some extent and also altered in some respects.

Stilesia, Railliet, 1893. Type species, Stylesia globipunctata (Rivolta), Railliet, 1893. Head with four suckers, but without hooks. Strobila thin and narrow. Genital pores irregularly alternate. Segments broader than long. Two distinct sets of testicles present in each segment, one on each side, but no testicles in the median line. Ovarium on the pore side. No vitelline gland, no shell-gland. Uterus double, finally void of eggs, which are contained in egg-pouches (paruterine organ). The genital canals pass dorsally of the nerve and of the ventral canal, and ventrally of the dorsal canal. Eggs with two envelopes. Habitat: Intestine of sheep, goat, and dromedary, and bile-ducts of sheep, goat, and South African wild antelopes (Africa, India, Italy, France).

In the genus as thus restricted, only St. globipunctata

(Riv.), vittata, Railliet, hepatica, Wolffhügel, and sjöstedti, Fuhrmann, remain. For Tænia centripunctata, Rivolta, a new genus must be erected, for which I propose the name Avitellina (to denote the absence of a vitelline gland).

Avitellina, nov. gen. Type species, Avitellina centripunctata (Rivolta). Head with four suckers, but without hooks. Strobila thin and narrow. Segments broader than long, flat in the proximal portion of the strobila, nearly cylindrical in the posterior portion. Genital pores irregularly alternate. Four distinct sets of testicles in each segment, one right and one left of each longitudinal canal, but no testicles in the middle field. Ovarium nearer the pore side; no vitelline gland, no shell gland; a single uterus. Eggs finally enclosed in egg-pouches (paruterine organ). The genital canals pass dorsally of the nerve and longitudinal canals. Eggs with two envelopes. Habitat: Intestine of sheep, Africa, Italy.

The genera and the hitherto described species of Stilesia and Avitellina can be recognised by the following key:

(1) Uterus single; a single paruterine organ; testicles in four groups; the genital canals pass dorsally of the dorsal canal. Avitellina, 4.

Uterus double; two paruterine organs; testicles in two groups; the genital canals pass ventrally of the dorsal canal. Stilesia, 2.

(2) Testicles all lateral to the ventral canal. 3.

Testicles mostly median or dorsal to the ventral canal. St. hepatica, Wolffhügel.

(3) The vas deferens forms a dense packet of convolutions (functionally a vesicula seminalis) between nerve and ventral canal before reaching the cirrus pouch; inhabits the small intestines of the dromedary. St. vittata, Railliet.

The vas deferens forms at the most three or four loose convolutions between the nerve and the ventral canal before reaching the cirrus pouch; inhabits the intestines of sheep and goat. St. globipunctata (Rivolta).

(4) The vas deferens runs its entire length dorsal to the

testicles; length two to three metres; inhabits the intestine of sheep. Only known species: A. centripunctata (Rivolta).

Stilesia hepatica, Wolffhügel, 1903. Figs. 14–16; Text-fig. 1.

Synonomy.

Stilesia hepatica, Wolffhügel, 1903.
Stilesia hepatica, Wolffhügel, Gough, 1908.
Stilesia sjöstedti, Fuhrmann, 1909.

Literature.

Wolffhügel.—"Stilesia hepatica nov. spec. ein Bandwurm aus den Gallengängen von Schafen und Ziegen Ostafrikas." 'Berliner Tierärzlichen Zeitschrift,' 1903, No. 43.

Gough.—"Notes on South African Parasites." 'S.A.A.A.S.,' Grahamstown, 1908.

Gough.—"The Anatomy of Stilesia centripunctata (Rivolta)." 'The Veterinary Bacteriological Laboratories of the Transvaal,' Pretoria, 1909.

Fuhrmann.—"Cestodes." 'Schwedische Expedition nach dem Kilimandjaro.' 1909.

Habitat.—Bile-ducts of sheep, goats, and wild ruminants in South, East, and Central Africa.

[Note.—Although Stilesia hepatica, Wolffhügel, is not the type species of the genus, I propose to consider it first, as its anatomy is very much better known than that of Stilesia globipunctata (Rivolta), the type species; the anatomy of all known species of Stilesia is, as far as yet worked out, very constant, only differing in minor points. As a description at full length is necessary only for one of the species, only the points in which the other three differ will be found under their respective headings.]

Stilesia hepatica was described in 1903 by Wolffhügel as being double-pored, and as differing chiefly in that respect from Stilesia globipunctata (Rivolta).

When working in the Transvaal I repeatedly had to deal with a Stilesia infesting the bile-ducts of sheep, which I identified with Stilesia hepatica, Wolffhügel, although

all the specimens that passed through my hands were invariably single-pored. In 1908, in a paper read before the South African Association for the Advancement of Science, at Grahamstown, C.C., I stated that Stilesia hepatica, Wolffhügel, was single-pored, and that the original description given by the author was at fault. Since then, by the kindness of Prof. Colin, I have been able to examine the type specimens of Stilesia hepatica, Wolffhügel. There is no possible doubt; the type specimens are certainly single-pored, with irregularly alternating pores. The anatomy of the worm differs considerably also in other respects from the data given by Wolffhügel. In the following the anatomy of the worm is given entirely on my own observations on fresh material, supplemented by re-examination of the type.

The worm invariably inhabits the bile-ducts, never the intestine. It occurs in sheep, goats, duiker (Cephalopus), roan antelope (Hippotragus equinus), Hippotragus sylvaticus meruensis, fide Fuhrmann, and various other wild ruminants occurring in South, East, and Central Africa. The scolex is almost invariably lodged in the peripheral capillaries of the bile-ducts. The parasites are often present in large numbers, dilating the bile-ducts; their presence does not cause calcification of the ducts, as Distomum hepaticum, L., does, but only a thickening of the tissues of the ducts. They appear to do otherwise but little injury to the host; almost all adult sheep in the Transvaal are affected.

Stilesia hepatica, Wolffhügel, is probably primarily parasitic in wild ruminants, and can be supposed to have adapted itself secondarily to sheep. The absence of records of the conspicuous parasite from other parts of the world, its occurrence in the wild antelopes, which are so characteristic of the Ethiopian region, and the wide range in its choice of hosts, would seem to speak for the probability of its not being originally a parasite of sheep.

Stilesia hepatica, Wolffhügel, is extremely contractile, more so than most other cestodes I have handled hitherto.

As one very rarely succeeds in extracting a worm entire its total length is very difficult to estimate, but it is probably between twenty and fifty centimetres. In life, when expanded, it is thin, gelatinous in appearance, semi-transparent, the edges of the strobila being serrated on account of the projection of the posterior angles of the segments. Against a black surface, the middle field appears clear, the lateral fields more or less opaque. In older segments in the posterior portion of the strobila, the uteri and paruterine organs show up as an opaque spot on each side of each proglottid; when contracted, the worm is thick, with frilled edges, and more or less opaque.

The scolex has four suckers, directed outwards and forwards. Very frequently the head is followed by what appears to be a thick "neck," 2 mm. in length, as broad as, or even slightly broader, than the scolex; behind this "neck" the strobila suddenly narrows to half the width. Examinations of the "neck" (in sections), however, reveals the fact that it is composed of young segments, and consequently belongs to the strobila and not to the scolex. The contraction of the first two millimetres of the strobila is of extremely regular occurrence, so much so as to cause remark, when one, as occasionally happens, comes across a worm not contracted in this way. As the scolex is usually lodged in a capillary of the bile-duct the swelling of the anterior portion of the strobila can be of use to the worm as an aid to the suckers, helping to anchor the worm by gripping the sides of the duct. Wolffhügel figures a scolex in his paper, which he states may belong to Stilesia hepatica; although the scolex in question is not followed by the contraction of the anterior portion of the strobila, I see no reason to doubt its belonging to this species.

The swelling of the portion of the strobila directly posterior to the scolex in Stilesia hepatica, Wolffhügel, on account of its probable function, can probably be compared to the pseudo-scolices of Idiogenes and Fimbriaria, and be considered as representing the first step towards the

acquisition of a pseudo-scolex. A fundamental difference is, however, that in Stilesia all segments must have passed through the pseudo-neck during the course of their development, whereas it is usually accepted that a true pseudo-scolex is formed after the fertile segments have been produced, and that the segments composing a pseudo-scolex remain sterile. The habit of contracting the youngest segments appears to be an old acquisition in the genus Stilesia; a scolex of Stilesia globipunctata (Rivolta), is illustrated in fig. 12, showing a similar contraction of the anterior portion of the strobila, though in a less degree.

The segments are much shorter than wide, and about twice as wide as thick. The width of the strobila varies from one to two or three millimetres. The posterior segments are longer than the anterior. The posterior margin of each segment surrounds, collar-like, the anterior end of the following, except at the middle of the segment. Segmentation is quite distinct (without sectioning) at 2·8 mm. from the scolex; the genital anlagen appear already at 9 mm.

The genital pores open near the middle of the lateral margin of the segment; they are single and irregularly alternate.

The cuticula does not appear smooth (as that of Avitellina centripunctata [Rivolta]), but is villous (in sections).

The longitudinal canals are both well developed. The lumen of the dorsal canal does not become obliterated. The ventral canal is situated lateral and ventral to the dorsal canal. At the posterior end of each segment transverse canals connect the ventral canals, forming a transverse ring, the dorsal and ventral branches forming a few anastomoses near the middle of the segment. The transverse canals arise from more than two, usually three or four openings in the ventral canal on its median side, and two or three lateral to the ventral canal; these last usually meet and form a lateral loop. The histology of the transverse canals is the same as of the ventral canal. They both have a thin membrane, produced by flat epithelial cells, surrounding the canal; these

cells in turn are in contact with the parenchyma, as described lower down for the excretory canals in the scolex of Avitellina centripunctata (Rivolta).

The dorsal canals do not appear to be connected by transverse commissures, nor to be connected to the ventral canals or their transverse commissures.

The lumen of the ventral canals measures up to 58 μ by 50 μ; the dorsal canals are about 30 μ by 25 μ in diameter.

According to the state of contraction, the course of the canals can vary from being nearly rectilinear to very closely spiral.

TEXT-FIG. 1.

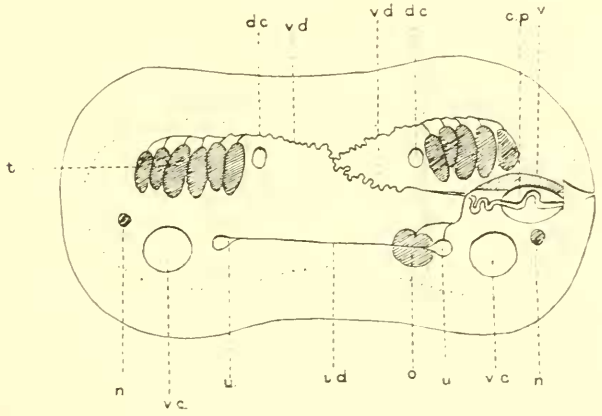

Diagram of Stilesia hepatica. (For explanation of letters see list of abbreviations at end of paper.)

Calcareous corpuscles are found in the medullary substance of the scolex and at the posterior ends of the segments; their diameter is 10 μ.

The muscles of the strobila are not very strongly developed. The longitudinal muscles are in two layers, the inner consisting of bundles of about twelve, the outer of three or four muscles. The transverse muscle is weak, as is also the dorso-ventral muscle.

The sexual organs differ greatly from Wolffhügel's description. In the first place each segment (of the type also!) has

but one pore, the pores being irregularly alternate. There is also only a single ovary to each segment, not two; and finally the arrangement of the testicles and vas deferens is quite different from what Wolffhügel described.

There are ten to twelve testicles on each side of the segment (fig. 13 and Text-fig. 1); they lie dorsally between the ventral and the dorsal canals, and dorsal to the ventral canal. Seen from the dorsal side of a total mount, the testicles lie in two or three rows of about four or five (sometimes six) in a row. On transverse sections (Text-fig. 1), one only sees a single row. The diameter of a testicle is about 50 to 55 μ. The vasa efferentia arise on the dorsal side of the testicles, as do the vasa deferentia. The vas deferens of the testicles on the right side of the proglottid runs from right to left, the vas deferens collecting from the left group of testicles from left to right; at the middle of the proglottid the left and right branches meet and join to form a common vas deferens which bends ventrally, and, having passed into the depth of the proglottid past the testicles, turns towards the pore side of the segment. It passes the dorsal canal ventrally, the ventral canal and nerve dorsally. Before reaching the cirrus pouch it forms a number of twists, whose function is that of a vesicula seminalis; these lie above the ventral canal. The cirrus pouch (fig. 16) is oblong, measuring 83 μ by 50 μ, the diameter of the cirrus 16·5 μ. Cirrus and vagina open into a wide and deep genital cloaca, whose aperture is situated near the middle of the segment.

The female organs also differ considerably from Wolffhügel's statements (fig. 13). There is but one ovarium, lying on the pore side, between the ventral and dorsal canals, nearer to the ventral than to the dorsal canal. The uterus is double, one uterus lying close to the ovarium, the other on the other side of the proglottid in the corresponding position. The two uteri are connected by a duct, the inter-uterine duct, which, however, may be morphologically but the median portion of the uterus. This duct crosses the ventral field ventral to the dorsal canal. The ovarium contains very few, at

the most fifty, eggs, measuring 14 μ in diameter; it atrophies very rapidly after the appearance of the uterus. (Wolffhügel's figure only shows the uteri, which have been erroneously labelled ovarium by him.) The ovarium measures 86 μ in diameter.

The oviduct, the uterine duct and the canalis seminalis meet a short distance from the receptaculum seminis, as in Avitellina. There is no vitelline gland, nor shell-gland. The function of the missing yolk-cells is exercised by abortive eggs in the ovarium (ovarial nutritive cells, see p. 371), and by cells derived from the uterine walls (uterine nutritive cells, see p. 375). The eggs in the uterus are firmly embedded in the uterine nutritive cells, as has also been observed by Fuhrmann (1909), who already suggested that their function is probably nutritive; however, contrary to his supposition, the uterus is originally hollow. The uterus measures 50 μ to 86 μ; the eggs are finally enclosed in paruterine organs similar to the paruterine organ described as occurring in Avitellina (see p. 375). The paruterine organ arises within the uterus; each segment contains two paruterine organs, one within each uterus. They measure 50 μ to 86 μ. The uteri and later on the paruterine organs are connected by a band of fibrous tissue, which covers the uterus anteriorly, passes through into the median field and tapers off towards the middle of the segment, the two halves of the band meeting in the middle. Their course across the segment is not quite direct, the middle portion drooping towards the posterior end of the proglottid. The eggs are enclosed in two envelopes, the outer of which invariably appears wrinkled whilst the inner is always smooth and rounded. The inner envelope seems to possess a prolongation at each pole (perhaps due to optical delusion and not existent; it is almost impossible to get rid of the outer envelope so as to examine the inner properly). The eggs, measured over the outer shell, are 26 μ long by 16 to 19 μ broad, the embryo 15 to 16 μ.

Wolffhügel states the size of the eggs as 26 μ × 16 μ, Fuhrmann as 16 μ (evidently only the embryo)!

Calcareous bodies are frequent in this species, as also in Stilesia globipunctata (Rivolta), and Stilesia vittata, Railliet; they measure on an average 10 μ in diameter, and are most frequent in the axis of the scolex, and at the posterior end of the segments. No calcareous corpuscles were observed in the type of Stilesia sjöstedti, Wolffhügel, but here, as elsewhere, this is probably only due to individual variation.

Stilesia globipunctata (Rivolta), 1874. Figs. 10, 11, 12.

Synonymy.

Tænia globipunctata, Rivolta, 1874.
Tænia ovipunctata, Rivolta, 1874.
Stilesia globipunctata (Rivolta), Railliet, 1893.
Stilesia globipunctata (Rivolta), Stiles, 1893.

Literature.

Rivolta.—'Sopra alcune specie di Tænia della Pecora,' Pisa, 1874.

Perroncito.—'I Parassiti dell'Uomo e degli Animali Utili,' Milano, 1882.

Perroncito.—'Trattato teorico-pratico sulle malattie piu communi degli Animali domestici,' Torino, 1886.

Railliet.—'Elements de Zoologie Médicale et Agricole,' Paris, 1886.

Neumann.—'Traité des Maladies parasitaires non-microbiennes des Animaux domestiques,' Paris, 1888 (1st edition).

Neumann.—"Observations sur les Ténias du Mouton," 'C. R. Soc. Hist. Nat., Toulouse,' 1891.

Neumann.—'Traité,' 2nd edit., 1892.

Stiles.—"Bemerkungen über Parasiten 17. Über die topographische Anatomie des Gefäss-systems in der Familie Tæniadæ," 'Centralblatt für Parasitologie,' 1893.

Stiles.—'Adult Cestodes of Cattle, Sheep, and allied Animals,' Washington, 1893.

Railliet.—'Elements,' 2nd edit.

Railliet.—"Sur quelques parasites du Dromadaire," 'C. R. Soc. Biol.," 1896.

Perroncito.—'Trattato teorico pratico,' 2nd edit., 1902.

Wolffhügel.—"Stilesia hepatica nov. spec. ein Bandwurm aus den Gallengängen von Schafen und Ziegen Ostafrikas," 'Berliner Tierärzlichen Wochenschr.,' 1903, No. 43.

Fuhrmann.—"Cestodes," 'Wissenschaftliche Ergebnisse der Schwe-

dischen zoologischen Expedition nach dem Kilimandjaro, dem Meru und den Umgebenden Masaisteppen deutsch Ostafrikas,' Stockholm, 1909.

Habitat.—Small intestine of sheep and goats. (Linstow's record from cattle in 'Compendium der Helminthologie' is a printer's error, as he is there citing Rivolta, who described the worm from sheep.

Geographical Distribution.—Italy, Rivolta, 1874; India (Giles *fide* Stiles, 1903—also specimens in Railliet's collection examined by the present author); France, Railliet, 1896.

For the following description I have had to rely considerably on Stiles (1893), the material at my disposal being rather badly macerated.

The worms are stated to be transparent, gelatinous in appearance when living, resembling *Stilesia hepatica*, Wolffhügel, in this respect.

The length varies from 45 to 60 cm., Railliet, 1896. The widest segments are 2·5 m.m. broad, the anterior and posterior being much narrower.

The scolex is square when viewed *en face*; it measures 0·768–0·9 mm. in diameter. The suckers (fig. 12) are directed anteriorly and diagonally; their opening is round or oval. The anterior portion of the strobila is sometimes contracted, as is more frequently the case in *Stilesia hepatica*, Wolffhügel.

The proglottids are always much broader than long, but in the posterior portion of the strobila are comparatively longer than in the middle of the worm. The middle portion is very frequently much contracted, the outline becoming crenate and twisted.

There are four to seven testicles on each side, lying lateral to the ventral canal, median to the nerve (fig. 10). The ovarium lies on the pore side, just median to the ventral canal; the uterus is double, one lying dorsal to the ovarium, the other close to the ventral canal of the other side of the body. The vagina lies dorsal to the cirrus pouch; it crosses the ventral canal dorsally; median to the ventral canal it increases

in size and forms a receptaculum seminis. The median end of the receptaculum seminis forms two branches, one of which, the oviduct, goes to the ovarium, the other, the uterine duct, goes to the uterus. (Do these two ducts arise directly from the receptaculum or from a canalis seminalis as in the other members of the group?) The uteri of both sides are probably connected as in St. hepatica, Wolffhügel, by an interuterine duct. The cirrus pouch is pyriform, 56 μ long by 40 μ broad, the cirrus 50 to 60 μ long. Cirrus and vagina open into a large and wide cloaca, which is directed diagonally lateral and forwards, opening near the anterior angle of the segment. Stiles observed the vas deferens to run from the cirrus-pouch anteriorly of the testicles of the pore side, dorsally of the ventral canal and female organs, ventrally of the dorsal canal, then through the median field, lying anterior and dorsal to the transverse canal; it is further stated to cross the dorsal canal (of the opposite side) ventrally, the ventral canal dorsally, and to be finally lost in the testicles. Should this last be correct, it would be a totally different course to that of the vas deferens in Stilesia hepatica, Wolffhügel; fresh material will have to decide this point.

The ovary contains but few eggs; there is no vitelline gland, and no shell-gland. The eggs enter the uterus fertilised; in the uterus they are surrounded by nutritive cells, as in St. hepatica, Wolffhügel. The eggs are finally enclosed in a paruterine organ. They have two envelopes, an outer wrinkled fusiform and an oval inner one; the inner one is devoid of spines (fig. 11). The spines in Stiles's figure are probably the shrivelled outer envelope. The eggs measure 56 $\mu \times 27$ μ over the onter, 27 $\mu \times 22$ μ over the inner envelope, 14 μ across the embryo.

The uteri of both sides, and later on the paruterine organs, are in contact with a band of fibrous tissue, which "extends partially around the uterus, crosses the dorsal canal ventrally, and tapers off into a fine point, which runs through the median field to meet," and is continuous with, the corresponding organ of the other side (Stiles, 1893, p. 78).

Stilesia vittata, Railliet, 1896. Figs. 8, 9.

Synonymy.

Stilesia vittata, Railliet, 1896.

Literature.

Railliet.—"Sur quelques parasites du Dromadaire." 'C. R. Soc. Biol.,' 1896, p. 491.

Habitat.—Small intestine of dromedary.

Geographical Distribution.—India. (Algiers? The type was collected in Alfort in a dromedary that died there, and a second batch was collected at the same place about two weeks after the first.)

Stilesia vittata, Railliet, so closely resembles Stilesia globipunctata (Rivolta), that Railliet, after describing the species, states that it may be only a variety of Stilesia globipunctata (Rivolta). However, certain constant differences can be found, if one may rely on Stiles's description of Stilesia globipunctata (Rivolta), and there appears to me to be no reason to doubt the correctness of that most accurate observer.

The worm has the same appearance (judging from formalin material) as Stilesia hepatica, Wolffhügel, and as Stilesia globipunctata (Rivolta). Its length is stated as being 18 to 23 cm., its breadth 1 mm. to 1·3 mm. In shape the scolex is similar to that of Stilesia globipunctata (Rivolta); however, when viewed en face the breadth (latero-lateral measurement) is somewhat greater than its thickness (dorso-ventral measurement). Its length is shorter than the breadth or thickness.

Three scolices measured were:

Broad .	(1) 0·60 mm. .	(2) 0·54 mm. .	(3) 0·55 mm.
Thick .	(1) 0·525 mm. .	(2) 0·48 mm. .	(3) 0·48 mm.
Long .	(1) 0·55 mm. .	(2) 0·375 mm. .	(3) 0·48 mm.

The shape of the proglottids is similar to that of the other two species, the posterior border of each segment overlapping the anterior end of the next proglottid in the same way.

There are five to seven testicles on each side, lying lateral to the ventral canal. The entire course of the vas deferens has not been made out, but the outer half of it runs ventral to the dorsal canal, and dorsal to the ventral canal and nerve. Between ventral canal and nerve the vas deferens forms a number of very close and densely packed convolutions, whose function is without doubt that of a vesicula seminalis (fig. 8, *v. s.*). In a "teased" specimen this packet of convolutions comes away entire. It appears almost to be enclosed in a membrane, but the material was too macerated to make quite sure.

The cirrus pouch measures 75 μ in length; it opens into a genital cloaca, which is directed laterally and anteriorly, and opens near the anterior angle of the proglottid.

The position of the female organs and their arrangement appears to be the same as in Stilesia globipunctata (Rivolta), the band of fibrous tissue between the uteri is, however, somewhat more strongly developed.

The muscles are arranged in two layers, the inner being composed of bundles of five to nine, the outer of only one to three.

The eggs have two envelopes, an outer shrivelled one and an inner oval or rounded one. They measure 38 $\mu \times 24$ μ over the outer, 22 μ over the inner envelope, the embryo measuring about 14 μ (fig. 9). (Railliet's measurements were 14–17 $\mu \times$ 13–17 μ.) The inner envelope is not provided with spines of any kind.

Avitellina centripunctata (Rivolta), 1874. Figs. 1 to 9, 17 to 35, 37 to 65. Text-fig. 2.

Synonymy.

Tænia centripunctata, Rivolta, 1874.
Stilesia centripunctata (Rivolta), Railliet, 1893.
Stilesia centripunctata (Rivolta), Stiles, 1893.
Stilesia centripunctata (Rivolta), Gough, 1909.

Literature.

Rivolta.—'Sopra alcune specie di Tænia della Pecora,' Pisa, 1874.
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Témpere.—"Parasites internes de l'homme et des Animaux domestiques," 'Micrographe Preparateur.' vol. xiv. 1906, p. 27.

Gough.—"Notes on some South African Parasites." 'S.A.A.A.S.' Grahamstown. 1908.

Gough.—"The Anatomy of Stilesia centripunctata (Rivolta)." 'The Veterinary Bacteriological Laboratories of the Transvaal.' Pretoria, 1909.

Habitat.—Small intestine of sheep.

Geographical Distribution.—Italy (Rivolta, 1874); Algiers (Railliet, 1891); South Africa (Gough, 1908).

In life the worm has a gelatinous, semi-transparent appearance. The strobila from 10 cm. from the scolex on appears longitudinally; there is a median opaque line, flanked on either side by a very transparent line (caused by the enormous ventral canals); laterally on each side the worm is again somewhat less transparent.

Avitellina centripunctata (Rivolta) reaches 202 cm. to 285 cm. in length. The greatest breadth is frequently, but not always, near the scolex. The breadth varies from 1 mm. to 3 mm. (or even 4 mm., Railliet). The anterior and middle of the strobila is flat, the posterior end is round or elliptical on section.

The scolex is large (fig. 7); in my specimens the suckers are invariably directed diagonally outwards and forwards. Railliet and Tempère, however, figure it with the suckers directed anteriorly. The scolex is usually, but not always, broader than long; it measures from 1·5 mm. to 2·8 mm. broad by 1·5 mm. to 3·1 mm. long.

The segments are always much broader than long, and usually also much broader than thick (except in the posterior portion of the strobila). The extreme brevity of the segments causes the genitalia at male maturity all to lie in one plane, single transverse sections 4 μ thick then often presenting the whole anatomy, as in a diagram. When the parnterine organ develops in the terminal portion of the strobila, the anterior and posterior surfaces of the segments are no longer flat, but are arched above the parnterine organ, bulging thus into the segments nearest in front and behind, and receiving depressions from the pressure of the paruterine organs of the segments anterior and posterior to it (fig. 3). Except at the posterior end of the strobila, the hind end of a proglottid does not surround the anterior end of the next.

The genital pores alternate irregularly; they are very slightly developed as compared to those of the Stilesiæ.

Calcareous corpuscles are extremely rare; two only have been observed in over one hundred series of sections.

The longitudinal muscles are apparently arranged in bundles of twenty-four or more, and a few solitary muscles are seen close to the subcuticula. The "bundles" are, however, not distinct on horizontal sections (see p. 352). The transverse and the dorso-ventral muscles are very weak.

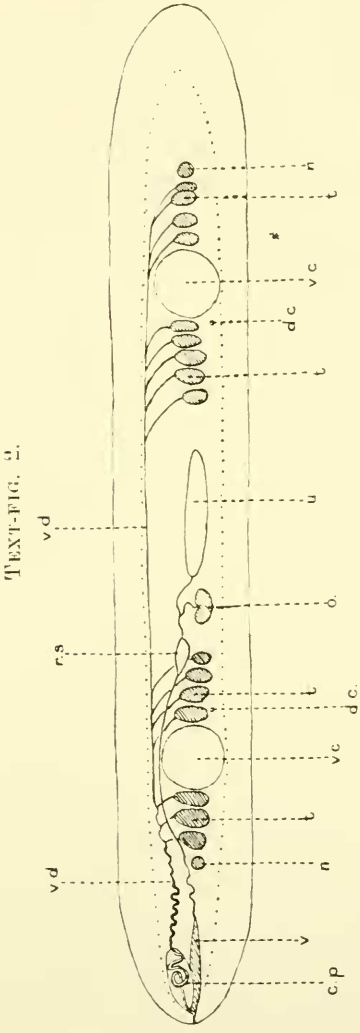
The ventral canals are very strongly developed in the strobila; their diameter varies from 72 μ at the apex of the scolex to 160 × 240 μ at 70 cm. from the scolex. The dorsal canal measures 72 μ at the apex, 32 μ at the base of the scolex. Its lumen is almost obliterated at 40 cm. from the scolex.

The course of the canals in the scolex is described further on.

The first traces of the genital organs are seen at 1 cm. from the scolex. The testicles are recognisable at 12 cm., the ovarium appears at 40 cm., male sexual maturity is reached at 70 cm.; at this stage the uterus begins to develop. The paruterine organs commence to develop at 90 cm.

There are three to six testicles on each side of each of the ventral canals, leaving a great gap in the middle of the segment

without testicles (fig. 1 and Text-fig. 2). The testicles lie slightly dorsal to the transverse axis. The vas deferens



TEXT-FIG. 2.

Diagram of Avitellina centripunctata. (List of abbreviations at end of paper.)

crosses the dorsal side of the median field, quite close to the transverse muscles, dorsal to the testicles, the nerve, the longitudinal canals, and to the female genitalia. Between the

ventral canal of the pore side and the cirrus-pouch it becomes distended with spermatozoa, and also slightly convoluted (vesicula seminalis). The cirrus pouch lies ventral or dorsal, anterior or posterior, to the vagina (figs. 4 and 43). The end of the cirrus is bent over and joins the vagina, it does not appear to be introduced into, but fused to the end of the vagina. There is a short and very narrow genital pore into which the vagina opens. The vagina runs straight to dorsal of the nerve and of the testicles; passing the ventral canal dorsally it widens median of the ventral canal (pore side) to form a receptaculum seminis. From the receptaculum seminis the canalis seminalis arises, which runs a short distance in the same direction as the axis of receptaculum would if lengthened; then it branches, one branch, the oviduct, turning ventrally towards the ovarium, the other, the uterine duct, also turning ventrally, leads to the uterus. The ovarium is bean-shaped, or kidney-shaped; it contains but few eggs. There is no vitelline gland nor shell-gland. The eggs pass through the oviduct into the uterine duct and then into the uterus, fertilisation taking place during the transit. The eggs receive nourishment from certain cells in the ovary and in the uterus (ovarial and uterine nutritive cells, pp. 371, 375). The eggs are finally enclosed in a parnterine organ, which arises within the uterus. Pads of fibrous tissue, lying anterior to the uteri, serve as support to the paruterine organs, and help to separate the genitalia of adjacent segments.

The eggs are enclosed in two spherical envelopes; the outer measures 40 μ, the inner 23 μ, the embryo 19 μ (fig. 2).

The Systematic Position of the Genera Stilesia and Avitellina.

Fuhrmann (1908) placed Stilesia together with Thysanosoma in a new sub-family which he called Thysanosominæ.

Now that the anatomy of the species of Stilesia and Avitellina are so much better known than they used to be,

it becomes necessary to review their position, and to see how far they are related to Thysanosoma.

The points common to the three genera Stilesia, Avitellina and Thysanosoma are: the marginal arrangement of the testicles, the irregular alternation of the single genital pores (which does not hold good for Thysanosoma, double-pored specimens being frequently met with in South Africa) and the possession of a paruterine organ. They differ, however, in several very important points: Avitellina and Stilesia do not possess either a shell-gland or a vitelline gland; their eggs receive nourishment from nutritive cells in the ovarium and in the uterus.

The points in which the three genera agree are hardly of sufficient importance to weigh very heavily; the position of the testicles and of the genital pores is liable to vary considerably within a sub-family; the possession of a paruterine organ can, as shown by Fuhrmann (1908), be acquired independently by genera belonging to various sub-families.

The lack of a vitellogene gland and shell-gland and the results of their absence are, however, quite sufficient to separate the two genera from all other known cestodes. I therefore propose to separate the genera Stilesia and Avitellina from the Thysanosominæ and to place them in a new sub-family of the Anoplocephalidæ, calling the new sub-family Avitellininæ, after the genus Avitellina, which is certainly the better known of the two genera.

Diagnosis of the Avitellininæ.—Scolex without hooks with four suckers. Segments short, genital pores irregularly alternating, testicles in two or four groups, marginal, none in the middle field. A single ovarium, no vitelline gland, no shell gland; uterus single or double, eggs finally enclosed in a paruterine organ. Eggs in ovary and uterus surrounded (and nourished) by nutritive cells. Oncosphære with two envelopes. Type genus, Avitellina, Gough, 1910. All the known species inhabit Ruminants, development unknown.

An Account of the Histology of Avitellina centripunctata (Rivolta).

Avitellina centripunctata (Rivolta) is on account of the large size of its histological elements and the loosenesss of their arrangement, exceptionally favourable for study.

The best results were obtained from worms fixed with Zenker's solution. I allow the solution to act for at least six hours, then I transfer the specimens to running water for twenty-four hours, after which they are carried through alcohol 25 per cent. and 50 per cent., remaining in each for at least three hours, being finally preserved in alcohol 75 per cent.

In order to obtain the worms as expanded as possible, I usually hold them up with a pincette, allowing them to hang free in the air; this almost instantly causes them to expand on account of their own weight, when I suddenly plunge them into the fluid, lifting them out at once; after letting them hang again for a few seconds I finally deposit them in the reagent. The worms treated in this way fix in a fairly expanded condition, and are not contorted or twisted. It is of great importance, however, to obtain the specimens alive, and they ought not to be washed previous to fixing. It is not necessary to use iodine to remove the last traces of sublimate from material treated in the manner described.

I have used sublimate, formalin, and silver nitrate, as well as Zenker, but no other reagent I know is to be compared with Zenker's solution for fixing cestodes. It is specially favourable for the study of the subcuticula and its connection with the muscles.

Staining was performed with Ehrlich's hæmatoxylin and orange G, which gives wonderfully clear pictures of the subcuticula and muscles. For the study of the eggs, and the changes taking place before maturation and fertilisation, I recommend iron-hæmatoxylin and eosin. This combination also presents the best results for the flame-cells and the nephridial cells surrounding the dorsal canal, and also shows

up the structure of the longitudinal muscles very distinctly. I have also employed hæmatein Apathy and Delafield's hæmatoxylin with good results. In using the Delafield one can obtain much the same results for the subcuticular cells as with Ehrlich's hæmatoxylin if, instead of differentiating with acidulated alcohol and blueing with ammoniated alcohol, one washes the specimens after staining in running water only. The nuclear structures do not stain as cleanly, however, as they do when using the stain in the ordinary way.

For specimens mounted in toto I use borax carmine; most of my material has been stained with borax carmine before cutting, being re-stained with hæmatoxylin after sectioning. I do not find that this spoils the final result; on the contrary, one often finds that the borax carmine helps to differentiate the nucleoli from the chromatin bodies in the nuclei.

My sections are invariably 4 μ thick, which appears to be the best thickness for Avitellina material.

Almost all the drawings have been made with the Leitz oil-immersion $\frac{1}{12}$ and ocular 2, and are reproduced as far as possible at the same scale.

I have made sections of Tænia serrata, Goeze; Anoplocephala magna (Abilgaard); Dipylidium caninum, L., and Stilesia hepatica, Wolffhügel, in order to obtain comparative material fixed, hardened, and stained in the same way. It was unfortunately not possible to obtain Ligula material.

The Cuticula. Figs. 17–21.

The cuticula consists of the usual two layers, which seem to have been observed by all recent observers, namely, a thin outer layer (Comidien Schicht, Minckert, 1906) and a thick inner layer (Homogene Schicht, Minckert, 1906), within which lies the extremely thin basal membrane (Grenzstreifen, Minckert).

The outer layer, or comidial layer, stains very deeply with hæmatoxylin; it does not appear to be provided with fine

hairs or other such structures. A fine radial striation is, however, readily observable in favourable sections (fig. 17). The thickness of this layer is from 1 μ to 1·5 μ. The comidial layer easily becomes detached, and is then sloughed.

The homogeneous layer is 3 μ thick on the average. Unlike the outer layer, it hardly stains with hæmatoxylin, but takes orange G or eosin readily. It appears (when fixed by "Zenker") to be quite structureless, except on the suckers, but impregnation with silver shows a definite structure also elsewhere. I have not been able to find any structures which can be compared to Minckert's (1906) trophopores, trophoporelles, neurophyses, or neuropores in the homogeneous layer of Avitellina centripunctata (Rivolta), nor any signs of pores running from surface to surface through this layer. However, in specimens impregnated with silver there are minute black granules scattered through the homogeneous layer, not quite evenly distributed, but more crowded towards the basal membrane, more scattered towards the comidial layer (fig. 18). I have observed a similar structure of the cuticula in Dipylidium caninum, L., fixed with Zenker, stained with iron-hæmatoxylin, and counter-stained with eosin; here the homogeneous layer presents exactly the same appearance as that of Avitellina when fixed with silver nitrate. The granules must therefore represent a finest structure of the cuticula, and are probably not merely artefacts (silver precipitates), as I was at first inclined to believe.

Certain modifications of the homogeneous layer are, however, invariably present in the cuticula of the suckers. These remain constant whether the specimen was fixed with Zenker, silver nitrate, or formalin. The comidial layer presents no contrasts to elsewhere, but the inner half of the homogeneous layer appears spongy or reticulated (fig. 17). The reticulations are formed by fibres running mostly at right angles to the homogeneous stratum, and forming numerous anastomoses amongst themselves. These fibres may be continuous with the parenchyma fibres of the suckers, which they much

resemble, especially in silvered specimens. The reticulations formed by the fibres enclose cavities which are probably in connection with each other. This structure has only been found in Avitellina; I have not observed anything similar in the other species I have examined.

Within the homogeneous layer and separating it from the subcuticular muscles lies an extremely thin membrane, the basal membrane, which can usually be quite readily demonstrated. The basal membrane is generally accepted as being derived from the parenchyma.

The formation of the cuticula has recently been studied by Young (1908) in Cysticercus pisiformis; according to him, "The cuticula of Cysticercus pisiformis is developed from a groundwork of simple parenchyma fibrillæ by a deposition among them of a cement substance. There are no specialised fibrillæ or cellular processes concerned in its development. The fact that in its development the processes of the subcuticular cells take part does not in any way detract from the above statement, since primitively the subcuticular cells themselves are undifferentiated parenchyma cells." Further (p. 288), "The cuticula is formed before the differentiation of the subcuticular cells."

Young's opinions are totally opposed to Blochmann's (1896) and his followers, who consider the cuticula to be mainly a product of the subcuticular cells.

It can, however, be proved from adult cestodes that the cuticula is not derived from the subcuticula. There is no doubt as to the presence of a cuticula consisting of comidial and homogeneous layers on the surface of the suckers, yet there are no subcuticular cells in the suckers. I have been able to convince myself of their absence in Anoplocephala magna (Abilgaard), Tænia serrata, Goeze, Dipylidium caninum (L.), Stilesia hepatica Wolffhügel. Young (p. 225) also states, "The subcuticula cells are lacking in the suckers." In all these species the cuticula above the suckers is similar to that elsewhere, differing somewhat in this respect from Avitellina centripunctata (Rivolta). There being

no subcuticula in the suckers, the cuticula of the suckers must arise independently of the subcuticula.

Unfortunately neither Rössler (1902) nor Young (1908) has made any observations concerning the development of the suckers. Leuckart ('Parasiten des Menschen,' 2nd edition, vol. i, p. 445) states that their development commences by the formation of four hemispherical depressions of the cuticula in the substance of the "Kopfzapfen," representing the cavities of the suckers, and that the radial muscles arise out of the subcuticular cells. Gläser (1909) finds the suckers arising somewhat differently, already before the subcuticula is formed, at least he avoids using the term "subcuticula." Leuckart considers that the fact of the development of muscles out of the subcuticular cells of the suckers is evidence that the subcuticula has nearer affinity to the musculature than to the epidermoidal apparatus. In discussing the subcuticula I will have to show that the subcuticula of the proglottids stands in very close relationship to both the dorso-ventral and to the transverse muscles; Leuckart's observation of the development of the radial muscles out of subcuticular cells would contain nothing very remarkable, as the subcuticular cells are actually muscle-elements.

If, as according to Blochmann, the cuticula is a product of an epithelial layer, and the subcuticula is that layer, then no cuticula can exist where there is no subcuticula. There is, however, no subcuticula in the suckers, and yet the suckers are clothed with a cuticula; the subcuticula cannot therefore be the epithelium producing the cuticula.

Cuticula with no underlying subcuticula is also to be found in older portions of the strobila, in segments where the paruterine organ is fully developed; but here we have not to deal with primary but with secondary conditions. In the anterior portion of the strobila the dorsal and ventral surfaces of the segments are more or less parallel to each other (fig. 43); proceeding distally we find that the segments are broader at their posterior than at their anterior end, the strobila appearing serrated on longitudinal sections. Examina-

tion of a single section (fig. 21) shows that dorsally and ventrally the following changes have taken place. The original cuticula, together with the subcuticula, has shifted its position from parallel to the longitudinal axis to one at right angles to the long axis, pivotting on the posterior border of the segment, the margin originally anterior having become the outer margin. The space between the outer margin, the anterior margin and the posterior border of the segment has filled with parenchyma; the new surface from the anterior border to the outer margin is clothed with a thin cuticula, under which there is no subcuticula. This cuticula may have been derived by stretching of the already present cuticula, or it may be of new origin; the fact that the cuticula covering the subcuticula now on the posterior surface is enormously thickened (by contraction?) would suggest that the cuticula covering the new surface is of new origin. The new cuticula only measures 1·5 μ to 1·7 μ that on the posterior surface is much folded, and measures up to 9 μ. The subcuticular muscles are also much more evident than usual on the posterior surface, the whole giving the impression that the cuticula and muscles have been compressed laterally (i.e. in the plane of the surface of the cuticula), thus causing the increase in thickness.

The Subcuticula. Figs. 19–21.

The subcuticula is present everywhere in a single layer close under the cuticula, except in the suckers and places mentioned above. It consists of a stratum of elongate cells, standing vertically to the cuticula. Its component cells are widely separated from each other, or densely congregated, according to the state of contraction of the worm. In shape they usually taper slowly towards the cuticula and are rounded or tapering towards the parenchyma (figs. 19, 20). Before reaching the cuticula several branches are usually formed, so that each cell touches the cuticula in more places than one. The outline of the cell is extremely distinct in properly fixed and hardened material; a thin membrane is

possibly present. The plasma is finely granular, staining readily with hæmatoxylin. The nucleus is oval, clear, surrounded by a distinct membrane, and contains a nucleolus and usually four chromatin bodies. The nucleolus stains differently to the chromatin bodies, my material being mostly stained in toto with borax carmine, and stained in section with Ehrlich's haematoxylin, counter-stained with orange G, the nucleolus staining reddish, the chromatin blue. Whether conical or rounded towards the parenchyma, each subcuticular cell gives off one or more fibrillar processes, which run inwards; the processes from several adjacent cells usually converge and collectively join the dorso-ventral muscles, where those muscles break through the longitudinal muscle (fig. 20). The subcuticular cells on the extreme lateral margin also behave in the same manner, only that they join the transverse muscle. Towards the lateral margins the connection between the dorsal or ventral subcuticular cells and the muscles is even more apparent, as the cells lie grouped around the base of the muscles, the subcuticular elements belonging to any one of the outer dorso-ventral muscles all lying lateral to their muscle, thus assuming a direction oblique to the cuticula.

I have been able to verify this connection between subcuticular cells and muscles in Dipylidium, Tænia, Dibothriocephalus and Triænophorus. The subcuticular cells consequently belong to the dorso-ventral and transverse muscle systems. In well preserved material it is possible to demonstrate this connection of muscles and subcuticula for every cell lying entirely in the plane of the section.

The question arises, Why have such processes not been observed before? In my opinion this is probably due to the methods used for fixing and hardening, and to the necessity to cut the sections in the plane of the cells. The subcuticular cells appear to be very difficult to fix and harden satisfactorily, Zenker's solution being the only one which has given me such results as yet. The silver impregnation method em-

ployed by Zernecke is probably not quite satisfactory, apart from its capriciousness and unreliability.

In older proglottids the subcuticular cells atrophy, their nuclei becoming smaller, their nucleolus and chromatin forming apparently a single mass filling the entire nucleus; and the outlines of the cells themselves become indistinct (fig. 21).

Having shown that the subcuticula belongs to the dorso-ventral and transverse muscle systems, and that the cuticula of the suckers arises independently of a subcuticula, and bearing in mind Young's observation of the development of the cuticula in Cysticercus prior to the differentiation of the subcuticular cells, it will be seen that serious doubts must again arise concerning the epithelial nature of the subcuticula. Balss (1908) also opposes the theory that the subcuticula is an ectodermal epithelium; he considers both cuticula and subcuticula to be of mesodermal origin, but he still admits that the cuticula is a product of the subcuticula. Of course the mere fact that the subcuticular cells form part of the dorso-ventral and transverse muscles would not induce me to deny their epithelial nature and their being the producers of the cuticula; remembering the epithelial muscles of hydroids, etc., it is mainly on account of the cuticula being formed in places where there is no subcuticula.

The Muscles. Figs. 22–29.

The muscles in the strobila, scolex, and suckers can everywhere be divided into the two groups, subcuticular muscles and parenchyma muscles.

The subcuticular muscles form two layers, whose fibres run at right angles to each other; the outer of these is situated very close to the cuticula, and runs horizontally, the inner runs longitudinally.

The parenchyma muscles in the strobila form three distinct muscle systems—the dorso-ventral, the transverse, and the longitudinal muscle systems. The first two are much weaker than the last.

The muscles in the scolex are more complicated than those in the strobila, as their course is modified by the suckers, and their requirements (Lühe, 1894). The following systems of muscles have been made out in connection with the suckers of Avitellina centripunctata (Rivolta).

Commencing at the apex of the scolex, and proceeding towards the strobila, we meet:

(1) A diagonal cross-system anterior to the terminal loops of the excretory canals; it covers the entire anterior surface of the scolex, passing from the front of the left ventral to the front of the right dorsal sucker, and from the front of the right ventral to the front of the left dorsal sucker.

(2) A second diagonal cross system, composed of four bundles of muscles, each consisting of only a few fibres, is situated just posterior to the terminal loops of the ventral canals; it runs from sucker to sucker in such a way as to connect—

(A) The median face of the right ventral sucker with the lateral face of the left dorsal sucker.

(B) The lateral face of the right ventral sucker with the median face of the left dorsal sucker.

(C) The median face of the left ventral sucker with the lateral face of the right dorsal sucker.

(D) The lateral face of the left ventral sucker with the median face of the right dorsal sucker.

(3) An orthagonal cross-system, running dorso-ventral and transversely, is situated just behind the second diagonal cross system and between it and the great nerve commissures. It connects:

(A) The median faces of the two left suckers.

(B) The median faces of the two right suckers.

(C) The lateral faces of the two dorsal suckers.

(D) The lateral faces of the two ventral suckers.

(4) A second orthagonal cross-system is situated behind the nerve commissure, near the base of the suckers. Its insertions correspond to those of the previous orthagonal system.

(5) Near their base the suckers are connected by a system of muscles, which connects the two dorsal suckers with each other and the two ventral suckers with each other, but does not seem to connect the dorsal with the ventral suckers. Its fibres connect:

(A) The right sides of the two dorsal suckers.

(B) The left sides of the two dorsal suckers.

(C) The right sides of the two ventral suckers.

(D) The left sides of the two ventral suckers.

The histological elements composing the parenchyma muscles can be divided into the following groups:

(1) Bipolar myoblasts with terminal fibrillæ.

(2) Bipolar myoblasts with lateral fibrillæ.

(3) Elongate bipolar myoblasts lying axially within the tubiform muscles of the longitudinal muscles.

The first group I have only found in the dorso-ventral muscle; the second forms the transverse muscle, and occasionally occurs in the dorso-ventral muscle; the third occurs in the longitudinal muscle.

(1) The bipolar myoblasts with terminal fibrillæ occur in all parts of the dorso-ventral muscle, and are its chief components. The cells are spindle-shaped, with an oval nucleus, whose long axis lies in the long axis of the cell (figs. 22, 23). The nucleus measures, on an average, $3{\cdot}5\,\mu \times 4{\cdot}25\,\mu$; it contains a nucleolus and two or more round chromatin bodies. The plasma stains deeply, and is sharply defined at the margins, as though enclosed by a membrane. At each end of these cells a fibrilla arises, which is several times longer than the cell itself; the fibrillæ are extremely thin, measuring only a fraction of a μ in diameter, they run in the general direction of the long axis of the cell; their course is, however, usually not quite straight, but sinuous or zig-zag. The fibrillæ may, perhaps, only act as tendons, in which case the cell would represent the contractile portion of the combination, but it is more probable that the fibrilla is itself contractile. These cells are usually found in rows, their fibrillæ lying in part apposed to each other, thus form-

ing the connection of the whole row to a muscle. The fibrillæ of the outermost myoblasts do not insert directly in the cuticula, but are in contact with the fibrillæ arising from the subcuticular cells.

Cells similar to these simplest myoblasts have been seen and described by Schiefferdecker (1874) in Tænia saginata, Küchenm.; he considered them to be connective elements; and by Hamann in Tænia (Mesocestoides) lineata, Rud., who described them as elements of the parenchyma.

(2) Bipolar myoblasts with lateral fibrillæ are, in Avitellina, chiefly found in the transverse muscle. They are the form of myoblast most frequently recorded by recent authors (e. g. Pinter, 1881; Hamann, 1882; Krämer, 1892; Will, 1893; Zernecke, 1895; Rössler, 1902; Young, 1908) in various genera and species. These muscle-cells differ from those described above inasmuch as the fibrilla runs continuously over one surface of the cell and does not originate only at the poles, otherwise they are very similar in appearance and dimensions (figs. 24, 25). Their nuclei measure $3{\cdot}5\,\mu \times 4{\cdot}25\,\mu$; their plasma is attached to the fibrilla, being widest at the middle and drawn out to a point at each pole. The plasma stains fairly deeply, and has a very distinct outline, probably being enclosed by a membrane. The fibrillæ are long, apparently homogeneous, and lie arranged parallel to each other. At the margins the fibrillæ of the transverse muscle spread fan-like towards the cuticula, as usual in other cestodes. Some of them appear to connect with the most lateral subcuticular cells. The fibrillæ are very thin, less than $1\,\mu$ in diameter. Young (1908), describing such myoblasts, states that the myoblast is always connected to the muscle by fibrillæ, even when the cell remains very close to the muscle. I have not been able to verify this observation in my material.

(3) The elongate bipolar myoblasts, lying axially in the tubiform muscles of the longitudinal muscles, are more difficult to observe than the other two varieties of

myoblast of Avitellina. The longitudinal muscles differ at first sight from the dorso-ventral and transverse muscles even under a low power, by the great development of the muscle-fibres; the myoblasts themselves are hard to find on account of their great length, which reaches as much as 65 μ or more, and on account of the length of the muscle-fibres, which can often be followed continuously through more than nine segments. Owing to their elongation, it too frequently happens that the myoblasts are not entirely contained in a single section, and owing to the large number of fibres in the longitudinal muscle it is hopeless to look for the continuation of such myoblasts in the next section.

The muscles are thick, measuring up to 9 μ in diameter, they are round or oval or even polygonal with rounded angles on transverse sections. On thin transverse sections a large number of the muscles, especially those of the outer layers, appear annuliform, having a clear space in the middle. Towards the inner layers of the transverse muscle, all the fibres are found to be solid. Zernecke (1896) figures such annuliform sections of the longitudinal muscles of Ligula, and I have found similar muscles in Dipylidium. The solid muscles are probably derived from tubiform muscles for the following reason. In sections stained with iron-hæmatoxylin, if favourably differentiated, the solid longitudinal muscles are seen to consist of a dark (black) staining core surrounded by a light outer sheath. This peculiarity can be observed in sections passing transversely to the muscles as well as in such running in the direction of the muscle and containing uncut muscles. As we will see later on, the tubiform muscles contain a portion of the axial myoblast in their hollow. If the myoblast deposits or produces the muscle substance, then the centre or axis of the muscle represents the younger deposit, which again stains differently to the outer portion. The fact that the annuliform sections very frequently do not contain any portion of the myoblast is probably due to shrinkage or contraction during fixation. If the solid muscles are the older ones, the outside position

of the annuliform muscles would indicate that the young muscles develop on the outside of the transverse muscle.

The myoblasts are bipolar, spindle-shaped and very elongate (figs. 26, 27); their nuclei resemble in most respects the nuclei of the myoblasts of the other two systems, but they are usually somewhat larger. Those measured averaged 4·25 μ to 5 μ long by 2·5 μ to 4·25 μ broad. The plasma is granular; a membrane appears to be present. The ends of the cells are inserted in the tubular ends of the muscles. In some cases the two tubiform muscles appear to be connected by a strip of muscle-tissue passing along one side of the myoblast. Similar muscles were observed by Salensky (1874) in Amphilina, although not re-found by either Hein (1904) nor by Cohn (1904) in the same object.

The longitudinal muscles appear to me to be produced by these cells, which in that case are true myoblasts, the contractile substance being formed or deposited on the surface of the cell, the body of the cell penetrating the axis of the muscle for a long time; then, as the muscle develops, its cavity becomes filled with muscle substance. In the end the cell disappears from the axis of the muscle, and becomes displaced so as to lie laterally to the muscle. Nuclei lateral to the muscles are frequently observed.

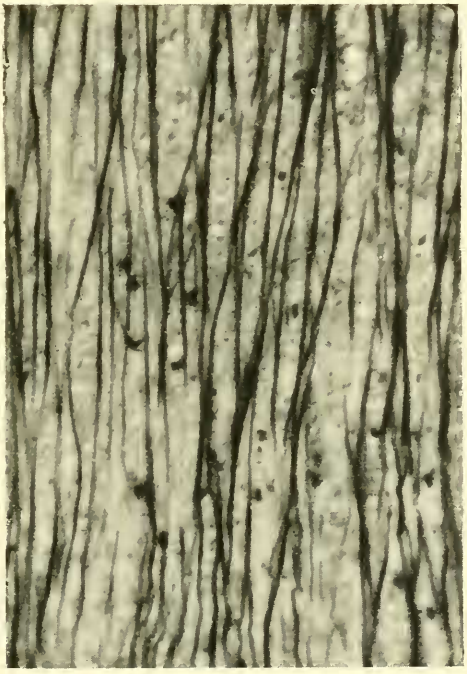
The muscle-fibres can be traced through a number of segments. Their course is not quite straight, but more or less sinuous. Text-fig. 3 is a photograph of a section cut parallel to the longitudinal axis of the worm, and represents a distance of about ten segments.

In transverse sections the muscles appear to be arranged in bundles, whose elements are more crowded towards the transverse muscle, more scattered towards the subcuticula. However, I distrust the appearance of the bundles, since it is impossible to re-discover them in horizontal sections (see Text-fig. 3). It will be seen that where a few muscles do group together, they receive fibres from the adjoining groups and give off fibres.

The schematic Text-figs. 4, 5, 6 will help to make my

meaning more clear. Fig. 4 shows the course of six muscles composed of bundles of four; one sees the sections of the dorso-ventral muscles separating the bundles. Text-figs. 5 and 6 have been drawn to show that it is possible to obtain transverse sections giving the appearance of bundles, but that

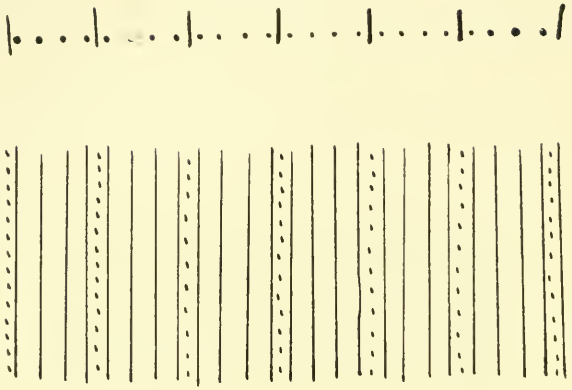
Text-fig. 3.



Horizontal section through the longitudinal muscle. About nine or ten segments are included in the photograph.

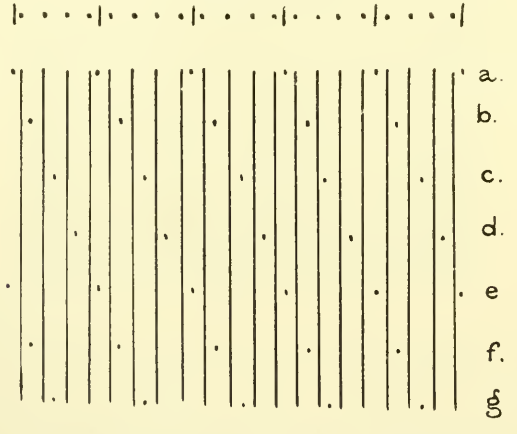
in each case the bundles at the levels *a*, *b*, *c*, *d* are differently composed. Thus at level *a*, 1, 2, 3, 4 form the first, 5, 6, 7, 8 the second, 9, 10, 11, 12 the third bundle, etc. At level *b*, 2, 3, 4, 5 form the first, 6, 7, 8, 9 the second, 10, 11, 12, 13 the third bundle. By the time level *e* is reached not a single fibre forming the first bundle is the same as at level *a*. The

TEXT-FIG. 4.



The top row represents a transverse section, the lower part of the figure a horizontal section. The figure shows the sections of the dorso-ventral muscles separating the bundles. The bundles are real.

TEXT-FIG. 5.



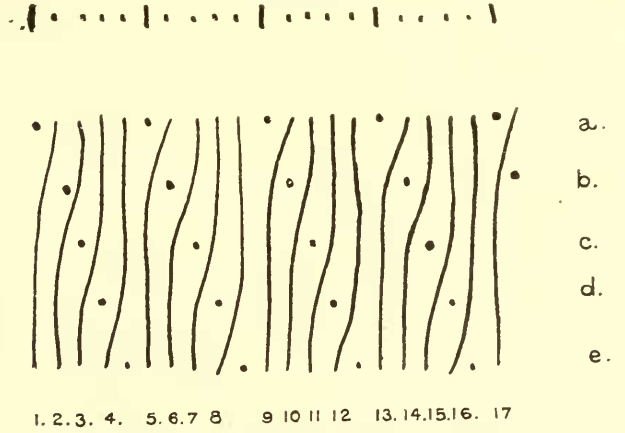
The top row represents a transverse section, the lower part of the figure a horizontal section. The figure shows the dorso-ventral muscles passing through between the longitudinal fibres. At the levels *a*, *b*, *c*, *d*, etc., one would find the muscles arranged in bundles of four, as in Text-fig. 4. The arrangement in bundles is only apparent.

number of fibres in a bundle and the number of bundles have remained the same, and if we were to judge entirely by transverse sections, we would have to conclude that the number of fibres in a bundle and the number of bundles is constant.

The fibres of the longitudinal muscle are apparently arranged in bundles of about twenty-four, with a few solitary muscles scattered near the subcuticula.

The subcuticular muscles arise, according to the usual view

TEXT-FIG. 6.



The figure represents a modification of the arrangement of the muscle-fibres shown in Text-fig. 5. The arrangement in bundles, as seen in transverse section, is only apparent.

as products of the "Sommer-Landois" cells, which are supposed to be myoblasts. Young (1908) opposes this view, as he finds the subcuticular muscles already formed before the "Sommer-Landois" cells are differentiated. Young consequently refuses to apply the term "myoblast" to them, and calls them "nenro-muscular" cells, because they send fibrillar processes into the muscles and because they are also connected with the nerves.

The "Sommer-Landois" cells of Avitellina are best examined in sections through the scolex. These cells send

one or two processes towards the cuticula to subcuticular muscles, and also one or two processes into the depth of the scolex to connect with the nerves (fig. 28). The nucleus is large, round, measuring 5 μ in diameter; it contains a nucleolus and a few chromatin bodies. The plasma is fibrillar in appearance, several fibrillæ uniting to form the processes leading to the subcuticular muscles or to the nerves. The whole cell has much more resemblance to a nerve-element than to a myoblast; it differs from the myoblasts of the parenchyma muscles in the obvious connection with the central nervous system, in being connected to more than one muscle-fibre, and in being multipolar instead of bipolar.

Young (1908) finds that the "Sommer-Landois" cells originate from cells similar to those I have described as occurring in the dorso-ventral muscle, and he lays importance on the fact that the muscles are present before the "myoblast" differentiates. The nerve-connection was observed already by Zernecke (1908) and Blochmann (1896) before Young. I consider Young to have been quite justified in giving the name "neuro-muscular cell" to the Sommer-Landois cells, as the cells are certainly quite as much nerve-elements as muscle-elements.

The Muscles of the Suckers.—It is possible to distinguish between parenchyma and subcuticular muscles in the suckers in the same way as in the rest of the body, the myoblasts and "neuro-muscular" or "Sommer-Landois" cells giving the clue to the group to which the muscles belong.

The radial fibres belong to the parenchyma muscles, the muscles just under the cuticula running parallel to the cuticula to the subcuticular muscles.

In Avitellina the radial muscles have lost their myoblasts, but in other forms examined by me (Tænia, Dipylidium, Cittotænia) it has been possible to readily demonstrate the presence of lateral myoblasts.

In Avitellina centripunctata (Rivolta), and in Anoplocephala magna (Abilgaard), there is a layer of cells

close to the cuticula of the suckers, separated from the cuticula by the superficial layer of muscles. This layer of cells does not represent the subcuticula, but rather must be homologised with the "Sommer-Landois" cells of the subcuticular muscles of other parts of the worm. The cells are more or less flattened, and lie in a plane parallel to the cuticula—subcuticular cells are perpendicular to the cuticular; these cells are multipolar (fig. 29), each cell sending out several processes, which either terminate in connection with muscle-fibres, or connect with processes from similar adjacent cells. The cells further stand in contact with the ganglion cells of the sucker by means of neuro-fibrillæ coming from the nerve-cells. The nuclei of the neuro-muscular cells in the suckers are oblong, small, measuring only 3·5 μ long. The points of resemblance between these cells and the "Sommer-Landois" cells are their connection with more than one muscle-fibre, their multipolarity, their connection with the central nervous system (of the sucker in this case).

Granted that these cells are really the homologa of the "Sommer-Landois" cells of the rest of the body, then the muscles they belong to must be subcuticular muscles, as "Sommer-Landois" cells have hitherto only been found connected to subcuticular cells.

The arrangement of the muscles in the suckers follows roughly the arrangement in the rest of the body; subcuticular muscles, in two layers, occupy the space directly under the cuticula, and are parallel to the cuticula; parenchyma muscles run perpendicular to the cuticula, and, in deeper layers, parallel to the cuticula.

The suckers are separated from the scolex by a delimiting membrane; directly within this membrane are two sets of fibres running parallel to it. The first set forms concentric rings, as can be seen on sections touching the base of the sucker; the second set radiates, the centre of the radiation being at approximately the same spot as the innermost of the concentric rings. These two sets lie close to each other, and remind one of the subcuticular muscles, which they possibly

are. Next to the subcuticula one also finds two sets of muscles; the outer is also composed of circular, concentric muscles, the inner of radial fibres. These two sets are without doubt subcuticular muscles; the "Sommer-Landois" cells mentioned above stand in contact with them. Between the cuticula and delimiting membrane are the radial fibres; in the middle of the thickness of the sucker there are other muscles, running at right angles to the radial fibres, whose course is possibly circular. These two last sets are without doubt parenchyma muscles.

Around the margin of the opening of the suckers the subcuticular circular muscles are much developed, forming a kind of sphincter.

It is worthy of remark that the subcuticular muscles of the suckers are much more developed in Avitellina and Anoplocephala than in Tænia and Dipylidium.

The Excretory System. Figs. 5, 6, 30–37.

The excretory system consists of the usual two pairs of longitudinal canals, the secondary transverse commissures, and of the flame cells and their capillaries.

In the strobila the ventral canal is enormously developed; it lies lateral to the dorsal canal, whose lumen almost atrophies in the posterior portion of the strobila.

Transverse commissures connect the ventral canals; they are not very readily observed in Avitellina centripunctata (Rivolta), but are wide and conspicuous in Stilesia hepatica, Wolffhügel, Stilesia vittata, Railliet, and Stilesia globipunctata (Rivolta), where they form a more or less complicated network at the posterior end of each segment.

The flame cells are very frequent in the medullary zone of Avitellina centripunctata (Rivolta), but extremely rare exterior to the transverse muscle. This is worth notice, as in other cestodes (Tænia serrata, Goeze, Dipylidium caninum [L.], and Ligula [fide Blochmann]) they seem to be very frequent among the subcuticular cells.

The course of the canals in the scolex is somewhat complicated, but can be reduced to quite a simple scheme. If it is remembered that the right and left halves only communicate by a single loop situated at the apex of the scolex, and that the dorsal and ventral canals of each side, after mounting through the scolex, meet and join each other just at the apical connecting loop, it will be seen that the whole can be reduced to the scheme given by v. Janicki for Inermicepsifer in a paper to be published shortly. The actual plan of the canals in the scolex is, however, complicated by the fact that the ventral canal forms a large number of loops and turns before reaching the apex. The course of the dorsal canals, on the other hand, is quite straight.

Before commencing the description of the course of the ventral canal it is necessary to explain the terminology to be used. I must distinguish between dorsal and ventral suckers, also between right and left suckers; the median face and the lateral face, the outer angle formed by two suckers and the inner angle formed by two suckers, and the base and apex of a sucker.

Dorsal and ventral require no further explanation; the median face of a sucker is that side which faces a line dividing the right dorsal and ventral suckers from the left dorsal and ventral suckers; similarly the lateral face is that side which looks towards the line separating the two dorsal from the two ventral suckers. The outer angle formed by two suckers is the angular space between the suckers near the subcuticula, the inner angle the corresponding space or angle opening on the medullary zone of the scolex. The base is the convex end, turned towards the strobila, and the apex the end of the sucker containing the mouth of the sucker (see diagram).

It has already been stated that the ventral canal in the proglottids lies lateral to the dorsal canal. Following the canals from the strobila into the scolex, we find that their relative positions change close to the scolex, the ventral canals lying internal to the dorsal canals.

The left ventral canal (fig. 5), on entering the scolex, turns

at right angles to its course, running horizontally towards the base of the dorsal sucker, then rising vertically it proceeds up the lateral surface of the sucker to the level of the bottom of the hollow of the sucker; it then turns over and proceeds downwards parallel to its ascent. Arriving near the base of the sucker it gives off a short branch, which runs towards the median outer surface of the sucker and terminates at the level of the bottom of the hollow of the sucker. The main canal re-crosses the base of the scolex horizontally, internal to and parallel to its first horizontal portion, but external to the dorsal canal, until it reaches the base of the left ventral sucker. It then ascends the median side of the left ventral sucker, almost to the mouth of the sucker, then turns again, running parallel to its former course until the base of the sucker is once more reached; it then passes around the external surface of the base of the sucker, forming a few spiral loops, until the outer lateral angle of the left suckers is reached. It then ascends the outer lateral angle, giving off a short blind branch towards the dorsal sucker at the level of the nerve commissure. Arrived near the summit of the scolex, it bends over and runs down the inner lateral angle of the left sucker until the level of the cross nerve commissure is reached; here it bends inwards, and then upwards past the nerve commissure, running ventral to and parallel to the dorsal canal until the apex of the scolex is reached. Here it bends over dorsally and fuses with (or is continued into) the dorsal canal. At the point of junction of the two canals the commissure connecting the right and left halves of the excretory canal system inserts. The dorsal canal is straight throughout its entire length.

The right ventral canal runs in a similar manner, at first ventral to and parallel to the right dorsal canal (fig. 6). Near the base of the suckers it also bends over dorsally, and, passing the dorsal canal externally, runs horizontally to the base of the right dorsal sucker, following the outer face of the sucker, which it ascends almost to its mouth, veering during this ascent more and more to the right.

Having ascended thus far, it again turns and descends parallel to its ascent; on reaching the base of the sucker it re-crosses the base of the scolex exterior to the dorsal canal, but interior to its first horizontal stretch. Arrived at the median internal side of the base of the right ventral sucker, it ascends the median ventral side of the sucker to the height of its mouth, then turns back parallel to the ascending portion of the canal. Passing around the base of the right ventral sucker internally, it ascends the outer angle of the two right suckers, sending off two blind branches towards the outer surfaces of the suckers at the level of the nerve commissure. The main canal continues its course parallel to the long axis of the worm to near the apex of the scolex; then it bends over, descends the inner angle of the right suckers until the nerve commissure is reached, when it bends over again, proceeding past the nerve commissure ventral to and parallel to the dorsal canal. Arrived at the summit of the scolex, it unites with the dorsal canal and with the connecting commissure in the same way as the left canal does. The right dorsal canal is straight throughout, agreeing in this respect with the left dorsal canal.

The "blind" branches given off by the ventral canals I have not been able to follow further than stated; of course, they may be much longer than their observed length. Bearing in mind the difficulty of tracing the transverse commissures in the proglottids of Avitellina centripunctata (Rivolta) for any length (I had not seen them at all in 1909), I certainly hesitate to say that a ring-canal is not formed; these branches may represent portions of a ring-canal, which, in that case, would be a transverse canal in the scolex homologous to the transverse commissures in the proglottids.

It is probable that the various loops change their course considerably according to the state of contraction of the scolex. Stilesia hepatica, Wolffhügel, also invariably shows a similar dorsal bend of the ventral canal at the base of the scolex; the entire course, however, I have not been able to study.

The ventral and dorsal canals are equal in diameter at the apex of the scolex, where they both measure 72 μ; proceeding away from the apex, or from the scolex, the ventral canal increases in diameter and the dorsal canal decreases. At the base of the scolex the ventral canal measures 128 μ in diameter, the dorsal 32 μ. At 10 cm. from the scolex the ventral canal was found to be 32 μ by 80 μ, the dorsal 16 μ by 32 μ; at 20 cm. the ventral canal measured 96 μ, the dorsal 28 μ by 20 μ; at 30 cm. the ventral had increased to 112 μ by 72 μ, the dorsal decreased to 4 μ. After this the dorsal canal becomes almost obliterated, whilst the ventral canal goes on increasing until it measures 160 μ by 240 μ, this size being reached at 70 cm. from the scolex.

The dimensions quoted show that the ventral canal is not always round on section; its shape varies considerably according to the state of contraction of the proglottid from round or oval to angular, square or polygonal sections being quite frequent in histologically perfect material. The ventral canal often occupies almost the entire thickness of the medullary substance, leaving scarcely enough space for the genital canals to pass.

The structure of the excretory canals varies according to the portion of the worm examined. A histological difference can also be observed between the dorsal and ventral canals in the strobila.

The longitudinal canals possess a fine membrane, which can occasionally be seen to be finely striated at right angles to the long axis of the canal. This membrane is the product of a layer of epithelial cells, which separate it from the parenchyma. These cells are best studied in the scolex; they are, as Bugge (1902) found in Moniezia expansa (Rud.), flat cells; their plasma is collected somewhat more above the nuclei than elsewhere, and their margins are not observable. Seen from the side, one observes that the layer is not equally thick everywhere, being thicker near the nuclei, thinner towards the margins. Exactly the same structure can be observed in Stilesia hepatica, Wolffhügel, where the

transverse canals present the same structure as the longitudinal canals.

I have not observed any special musculature of either the dorsal or the ventral canals in Avitellina.

In the strobila certain changes take place in the epithelial layer of the canals. The nuclei of the epithelial cells sink into the surrounding parenchyma, the membrane remaining connected to the epithelial cells by a fibrillar structure standing vertical to the surface of the canal (fig. 30). This arrangement is especially noticeable in the dorsal canal, but is also present in the ventral canal. Bugge (1898) figures the same radial arrangement of the fibres without comment.

Fig. 31 shows the dorsal canal at about 25 cm. from the scolex. The lumen has almost disappeared, being only 1 or 2 μ wide. The membrane has consequently thickened considerably, and is seen to consist of two layers, a thin dark-staining inner and a thick light-staining outer layer. The outer layer is followed by a darker layer with radial structure, whose fibres appear to be continuous with the radial fibres belonging to the epithelial cells; the epithelial cells have sunk considerably deep into the surrounding parenchyma. Their plasma shows a fibrillar structure, arranged radially where in contact with the canal, and less definitely around the nucleus. The plasma stains very lightly with orange G, but takes eosin deeply. The nucleolus is large, its membrane stains distinctly; it contains a nucleolus and one or two chromatin bodies. At first the cells appear to lie close to the radial fibres; then they grow in length and their nuclei move further away from the canal; the portion of the cell surrounding the nucleus becomes rounded or retort-shaped, the plasma becoming less dense as it recedes from the canal. A connection by its fibrillæ with the canal is always to be made out. In appearance these cells suggest glands, which swell and increase in size as they come into function. Their connection with the dorsal canal is always evident; the radial fibres surrounding the canal certainly belong to them, not to the parenchyma. In cells which have reached their full

development the radial fibres are seen to enter the cell and to be continuous with the fibrillar plasma. I consider these modified epithelial cells of the dorsal canals to be nephrocytes; they do not appear to have attracted the attention of other observers as yet. As no flame-cells arise from the dorsal canals they must represent the terminal nephridial element of the dorsal canals.

In the ventral canals a similar change takes place. The epithelial cells also sink into the surrounding parenchyma (fig. 30), remaining connected with the membrane by radial fibrillæ. They do not, however, become directly modified into gland-cells, but indirectly give rise to the flame-cells and their capillaries. Figs. 32, 33, and 36 show the development of the flame-cells. The first stage is represented by fig. 32; here we see a single epithelial cell sinking into the parenchyma, away from the membrane of the ventral canal, but remaining attached to the canal. The next change apparently takes place very rapidly, but without doubt it consists in the multiplication of the cell, a row of five nuclei, as shown on fig. 33, being produced. These five nuclei belong to four developing flame-cells and their capillary cell. A group of young flame-cells is to be seen on the same figure. The development of the flame-cells in *Avitellina* thus goes very much on the lines described by Bugge (1902), only here we have four flame-cells in a group instead of only three, the capillary cell in each case originating in the same way. As Bugge, I have only found developing flame-cells quite close to the ventral canal, never at any distance from it. Examination of *Tænia serrata* gives the same results, only in this species the flame-cells are in groups of three, plus one capillary cell (see fig. 36).

I cannot agree with Young (1908) that the flame-cells develop from parenchyma cells, and that "the capillary cell is at least a parenchyma cell of separate origin from the flame-cells, and that the capillary is formed at first as a passage in parenchyma strands, to become modified later into a definite tube with a specially modified wall." On the other

hand, every stage of the development of the flame-cells observed by me in Avitellina has served to verify Bugge's statements.

The fully developed flame-cells do not present any remarkable differences from those figured and described by other authors, except that they almost regularly contain a small corpuscle in the plasma, whose nature I have not been able to identify (*x*). The cells always occur in groups of four, most frequently in the medullary substance, very rarely in the transverse muscle, hardly ever exterior to the muscle. They consist of a cell (figs. 34 and 37) with granular plasma, usually with irregular, star-shaped outline; the nucleus contains a nucleolus and a varying number of chromatin bodies. The flame usually stands vertically to the cell, more rarely tangentially; the flame is often quite close to the nucleus, but it is sometimes separated from the main portion of the cell and the nucleus by a longer or shorter "neck" of plasma. The flame arises from a basal plate, a meniscus-shaped body with its concave side turned towards the flame, its convex side embedded in the cell. The flame itself consists of cilia. The funnel is widest a little way from its base; near its middle it is suddenly thickened, a ring of the substance of the funnel projecting into and somewhat constricting the lumen. The capillary usually runs straight in the same direction as the funnel for about once or twice the length of the funnel, and then bends suddenly to one side; after a short distance it bends again to resume its original direction. The capillaries can often be followed for a considerable distance, and frequently present a very devious course. It is interesting to note that the flame-cells invariably lie at right angles to the longitudinal axis of the worm, so that they fall within the plane of a transverse section. They are fairly frequent in the scolex as well as in the strobila, but do not occur in the suckers.

The flame-cells have long been recognised to be unicellular glands (Pinter, Lang, Bugge, Blochmann), and the capillaries to be their ducts; both the flame-cells and the nephrocytes

of the dorsal canal have a common origin—the epithelial cells of the excretory system.

The Nervous System. Figs. 38–40.

The central nervous system of the strobila consists of a nerve lying lateral to the ventral canal on either side of the strobila. From this main nerve branches are given off in every segment, which are, however, very difficult to observe.

The nerves on entering the scolex first bend inwards, passing well into the central space enclosed by the suckers. At the level of the bottom of the hollow of the suckers four ganglia are found, two lying in the inner lateral angles formed by the suckers, two in the inner median angles. These four ganglia are connected by transverse commissures, so that the lateral ganglion of each side is connected to both the dorsal and the ventral median ganglia; the ganglia are further connected by a transverse commissure, connecting the two lateral ganglia, and a dorso-ventral commissure, connecting the two median ganglia. The transverse and the dorso-ventral commissures fuse in the middle of the scolex, where they cross each other and form a central ganglion. Each of the four peripheral ganglia gives off two nerves, which proceed at first anteriorly and then bend over and unite with the nerve of the neighbouring ganglion, the eight nerves thus forming four loops connecting the four ganglia. Anterior to these is a second central nerve-plate, poorer in ganglion cells, whose connection with the rest of the nervous system has not been made out.

The histology of the nervous system presents on the whole the usual structures. The lateral nerves in the strobila consists chiefly of neurofibrillæ, arranged parallel to each other on longitudinal sections, having a reticulated appearance on transverse sections. The neurofibrillæ are accompanied by scattered glia cells, which are chiefly found on the surface of the nerve. Ganglion cells were very rarely observed in the nerves of the strobila.

In the ganglia of the scolex nerve-cells are very prominent, their large size and deep staining (with Ehrlich's hæmatoxylin) making them most conspicuous. Multipolar ganglion cells were most frequently met with in the ganglia, bipolar in the nerves.

The multipolar ganglion cells (fig. 38) have a reticulated or spongy protoplasma, which stains dark blue with the hæmatoxylin. From the processes of the cells the neurofibrillæ can often be traced for some distance. The nuclei measure 8 μ to 9 μ long by 4·5 μ to 8 μ broad; they are vesicular, and contain a large nucleolus (up to 2 μ in diameter) and one or two chromatin bodies. The nucleus itself is much paler than the surrounding plasma; the nucleolus stains rather lighter than the chromatin.

In the nerves arising from the scolex ganglia large bipolar ganglion cells are frequent; fig. 39 represents a portion of such a cell, one end not being in the plane of the section. The nucleus resembles that of a multipolar ganglion cell; the cell-plasma, however, contains tigroid bodies. From each end of the cell neurofibrillæ can be traced for a considerable distance. The long axis of the bipolar ganglion cells always lies in the direction of the nerve.

In the suckers one also finds large multipolar ganglion cells (fig. 40); they usually lie rather nearer to the delimiting membrane than to the cuticula; their processes usually unite with those of neighbouring nerve-cells, or they are connected with each other by their neurofibrillæ. A connection between the sucker ganglion cells and the "Sommer-Landois" cells of the subcuticular muscles of the suckers can frequently be made out.

The nuclei of the sucker ganglion cells measure from 6 μ to 7 μ in diameter; they are usually globular and contain a large nucleolus, measuring up to 2 μ, and one or two chromatin bodies. Small glia cells are frequent along the surface of the cell processes or the neurofibrillæ.

I am not aware that anyone has yet pointed out the presence of ganglion cells in the suckers; I have already mentioned

them as occurring in Stilesia centripunctata (Rivolta) and Anoplocephala magna (Abilgaard), (Gough, 1909). I have recently also observed similar cells in Tænia, only in Tænia they are smaller than in Anoplocephala or Avitellina, agreeing in this respect with the other scolex ganglion cells. Recently, similar cells have been observed by Spätlich (1909), in the bothridia of Tetrabothrium laccocephalus and T. macrocephalus; he describes them as being large cells with granular plasma, which stains deeply with hæmatoxylin, and with a large nucleus in which several large chromatin masses are visible. These cells have branched processes and form a reticulation between the muscle-fibres by the anastomosing of the processes. These branched cells are more or less restricted to the middle of the bothridia, keeping distance from either surface. Spätlich thought that they might be glands, but states that his material was not sufficiently well preserved to allow definite conclusions.

It is strange that nobody has yet looked for ganglion cells in the suckers, as they could be expected to exist in order to control the working of those complicated muscular organs.

The Genital Organs. Figs. 1–4 and 41–65; Text-fig. 2.

When the genital organs are in full activity, the receptaculum seminis is filled with spermatozoa and the oöcytes are passing from the ovarium into the uterus; the genital organs are disposed as shown on Text-fig. 2 or fig. 1. The position of the cirrus pouch to the vagina is extremely variable, as shown on fig. 43; it can lie anterior or posterior, dorsal or ventral to the vagina. The figure shows a sagittal section through about nine sections, passing through four cirri and vaginæ; it will be seen that the utmost possible irregularity has been realised.

The vagina leads into the spermiduct, which shortly after having crossed the ventral canal widens and forms the pear-shaped receptaculum seminis (Text-fig. 2); from the wider

interior end of the receptaculum seminis arises the canalis seminalis (Befruchtungskanal—fertilisation duct), which, however, soon branches, sending one arm, the oviduct, to the ovarium, the other arm, the uterine duct, to the uterus. Fertilisation of the eggs probably takes place at the point of junction of the three ducts, as one cannot observe spermatozoa penetrating into either the oviduct or the uterine duct. The uterus originates as a simple, hollow, transverse tube, but fills with cells soon after the arrival of the ova, cells derived from the uterine walls completely surrounding and embedding the eggs.

At the same time the male sexual organs consist of a cirrus, which opens straight into the vagina; the vas deferens forms several twists and turns within the cirrus-pouch (fig. 4). Just before entering the cirrus pouch the vas deferens is considerably swollen with spermatozoa, forming a kind of vesicula seminalis. The vas deferens runs straight across the dorsal side of the segment, being dorsal to all the other genital organs, to the nerve and to the excretory canals. The testicles lie near the transverse axis, in four groups of from three to seven testicles, one group being lateral and one median to each ventral canal.

The changes that follow as the segments proceed from the anterior end of the strobila to the posterior end are, first the disappearance of the ovary and oviduct, then of the canalis seminalis, then the testicles disappear. The uterine duct, the receptaculum seminis and the cirrus pouch with the vagina remain long after their function is past. When the ovary is disappearing the paruterine organ begins to develop; finally all the eggs are enclosed in the paruterine organ (fig. 3).

In their first anlage the cirrus-pouch and the vagina appear to have a common origin in a clump of dark-staining nuclei which collect near one of the lateral margins. Later on this clump splits into two masses, which are surrounded by myoblasts (fig. 44). In the middle of each of these masses a central core of cells differentiates, those which are

to form the vagina advancing in their development perhaps somewhat more rapidly than those from which the cirrus arises. The central core is at first solid, at this stage it cuts itself off from the surrounding cells by the formation of a basal membrane. The cavity arises by the cells separating in the middle of the epithelial cord. At this stage we find the vagina lined with an epithelium; later on the cells of the epithelium atrophy and their nuclei disappear. The fully developed vagina (fig. 45) is lined with fine cilia, all pointing away from the pore; it is surrounded by a sheath of large cells, with round, dark-staining nuclei. The plasma of these cells does not stain; their membranes are, however, very distinct. In shape, the cells are prismatic, with all the sides delimited by planes, the ends of the cells bordering on the parenchym generally forming pyramids. These cells surround the vagina in a single layer; their function may be glandular (?), and they certainly help to give greater rigidity to the vagina.

The female sexual canals, spermiduct, oviduct, uterine duct, canalis seminalis and the receptaculum seminis all arise as solid cords of epithelial cells, which, after having produced a basal membrane, become hollow. As is the case with the vagina, the epithelium atrophies, and finally disappears. Oviduct, canalis seminalis and uterine duct are, when completely developed, lined with cilia. The receptaculum seminis is not a simple dilation of the spermiduct due to the action of the contents, but arises out of a clump of cells which already show the final shape of the organ.

The ovarium forms at a very early stage a clump of darker staining cells near the middle of the medullary layer. It is remarkable, when fully developed, as compared with the ovaries of other cestodes, on account of its compactness, and also by reason of the fewness of the oöcytes produced. The ovary is bean- or kidney-shaped, the oviduct inserting in a depression of its dorsal side; it consists of a number of lobes, separated from each other by septa (fig. 41); the lobes are all enclosed by a common outer membrane. The single lobes do

not contain very many eggs; an ovarium produces at the most fifty to one hundred eggs, a lobe probably not more than one dozen. Besides the eggs, each ovarium contains a number of smaller cells, probably abortive oöcytes, which lie scattered between the eggs and along the walls of the lobes. Fig. 42 represents a single such cell lying between three oöcytes, which have not been completely drawn. For these cells I propose the name ovarial nutritive cells, on account of their probable function. They are much smaller than the oöcytes, and are fairly rich in plasma. In shape they accommodate themselves to the space at their disposal between the eggs. They are very extensively in contact with the eggs, sending out plasmatic processes along and over the surface of the surrounding oöcytes. Their nuclei are oblong, rather pale, especially as compared to those of the oöcytes, and contain a varying number of small round chromatin bodies. The diameter of a nucleus averages 17 μ by 9 μ.

There seems to me to be no possible doubt about the function of these cells. They act vicariously for the missing yolk-cells, and supply the oöcytes with nutriment by means of the processes touching and covering their surface. According to the accepted theory, the yolk-gland (vitelline gland) is only a modified ovarium, and the yolk-cells modified oöcytes. Should this theory be correct, it would render the mutation of oöcytes into nutritive cells within the ovarium easy to imagine, the chief difference from the state of things existing elsewhere being, that here both nutritive cell and oöcyte arise in the one ovary, elsewhere the oöcytes arise in the ovary and the nutritive cells (yolk-cells) in a modified ovary, the yolk-gland. A very important difference, however, still remains. The yolk-cell of other cestodes becomes attached to the oöcyte, and remains closely united to it for a long period after having handed over to the oöcyte its supply of yolk, being enclosed in the shell with the oöcyte. In Avitellina and Stilesia the nutritive cell is only temporarily connected with the oöcyte, it does not leave the ovarium when the oocyte does, and finally one nutritive cell

has relations to several oöcytes at the same time. For all that, ovarial nutritive cell and yolk cell have in common, that both are modified oöcytes. The fact that in Avitellina and Stilesia the ovarium has in some degree the double function of ovary and vitelline gland, might be taken as proving the two genera as being primitive.

The oöcytes appear to mature in the ovarium, the reduction of the chromatin taking place before the eggs leave the ovarium. In this respect they differ from the oöcytes of Tænia serrata, studied by Janicki (1907), which mature in the uterus after the penetration of the spermatozoon into the egg-cell. The process of ripening is complicated by the passing of chromatin out of the nucleus into the plasma. Spätlich (1909) observed somewhat similar phenomena in Tetrabothrium before the mitoses take place. For the study of these changes it is necessary to use material that has been stained with iron-hæmatoxylin, and to compare with sections stained by other means, as very much depends on the technique of the specimen. Figs. 57–65 show in a series of eggs the most important changes that take place before maturation and immediately after fertilisation. Fig. 57 is the youngest stage illustrated; it represents an oöcyte that has already reached its full size. Its plasma shows no modifications whatever, being perfectly homogeneous. A nucleolus is not visible; the chromatin forms a large round mass. Fig. 58 shows a somewhat older oöcyte; a nucleolus has appeared, and in the plasma two centrosomes can be observed. The centrosomes in the cestode oöcyte are quite large objects, as already observed by other authors (e. g. Janicki, 1907). When they first appear they have a light centre surrounded by a dark ring. On the same cell one sees that the chromatin is lying quite on the nuclear membrane, causing it to press out somewhat. Fig. 59 is also of about the same stage; in the cell shown a portion of the nucleus appeared to be cutting itself off from the main portion. I cannot say whether this is a regular occurrence or no, as I have only observed it in a single cell. The next changes are

shown on fig. 60; here we find that the size of the chromatin body in the nucleus is reduced, and that now there have appeared two dark-staining bodies in the plasma, lying quite close to the nucleus and just opposite the chromatin body. In iron-hæmatoxylin these bodies stain to the same intense black as the chromatin; with Delafield's hæmatoxylin they also stain blue, but not quite as deep as the chromatin. I consider them to be portions of the chromatin which have been ejected from the nucleus; in the course of the further development of the egg they behave as the yolk-nucleus observed by Janicki does. They are certainly not the same as the yolk-nucleus observed by Spätlich in *Tetrabothrium*. I have not seen any structure to compare with Spätlich's yolk-nucleus. There are usually only two of these problematic bodies present; occasionally, however, as shown by fig. 62, a larger number can appear. Whilst they were at first situated close to the nucleus, in older ovaria we find that they have moved further away from it, until they have gone as far as possible away from the oöcyte nucleus. Fig. 61 shows the emigrant chromatin bodies moving away from the nucleus, and shows that they have also separated from each other at the same time. A further change in the nucleus can be noted, the linin threads are becoming distinct. Figs. 63–65 show that a mitosis is now becoming imminent; the chromatin mass has entirely disappeared, and the chromatin has rearranged itself on the linin threads; the nucleolus, at first large, is reducing its size. But it is also remarkable that not only has the chromatin in the nucleus changed its arrangement, but also the chromatin that had wandered into the plasma. In the place where the emigrant chromatin bodies had been one now finds a mass of fine granules, and finally the only remaining trace is a darker staining of the plasma in the vicinity of the place they had occupied. It is worth noting that a pair of centrosomes are often seen close to the emigrant chromatin before it dissolves.

The mitoses that follow have been observed, but in specimens stained with Ehrlich's hæmatoxylin considerable luck

is necessary to obtain material where mitoses are taking place, as they pass very quickly. Usually only two or three segments at the most show mitoses; those before and after not containing any; the difficulty of obtaining sections through the exact portion of the strobila is consequently easy to appreciate. There appear to be four chromosomes, the exact number being hard to count, as the karyokinetic figure is very small. I have not been able to make out the fate of the pole bodies, but when the eggs pass into the oviduct they are no longer to be found. The matured oöcytes are not enclosed in a membrane of any kind; they arrive naked in the uterus, not having a membrane of their own, and not receiving a shell, as there is no shell-gland. The fertilised oöcytes are at first not enclosed in shells or by membranes. Fig. 49 shows four oöcytes in the uterus in various stages of development; in oöcytes *a* and *b* one sees the spermatozoa as short rod-shaped bodies, stained black by the hæmatoxylin, lying in a dark area, stained bright red by eosin. Oöcyte *c* shows the sperma nucleus and the egg nucleus fusing in the same manner as described by v. Janicki (1907) for the eggs of Tænia serrata. The plasma of the eggs in these first stages after fertilisation is not homogeneous, but contains larger and smaller masses of differently staining substance.

The later fate of the eggs has not been followed up; at first, however, the multiplication of the nuclei is not followed by division of the plasma, so that up to four nuclei can be seen in an undivided mass of plasma. Later on one observes quite regularly that the cell division gives rise to a few macromeres, and to a greater number of micromeres, the macromeres probably giving rise to the egg envelopes, the micromeres to the embryo, as demonstrated by Janicki (1907) for Tænia serrata. The exact number of macromeres is difficult to ascertain accurately: one is always larger than the others; two can usually be recognised, but I am not certain whether there is a third or no.

Soon after the eggs arrive in the uterus they become

surrounded by smaller cells, derived from the walls of the uterus. These cells, which have already been observed by Fuhrmann (1909) in Stilesia sjöstedti, Fuhrmann, can be termed uterine nutritive cells; their function is without doubt nutritive, as already suggested by Fuhrmann. The uterine nutritive cells (fig. 49) soon fill all the space between the eggs. They are rich in plasma at first; later on their plasma decreases, and finally they atrophy and disappear entirely at or before the stage when the egg envelopes have developed.

Fuhrmann (1909) supposed the uterus of Stilesia to have no cavity originally. This is not correct for Avitellina; the uterus is a simple hollow tube at the time of the arrival of the eggs, the uterine nutritive cells appearing shortly afterwards.

The absence of a vitelline gland, as can be seen, has had such an influence on the cestode as to have caused cells of two separate and distinct origins to arise in two different organs to replace to some extent the nutritive function of the missing organ, that is, if the vitelline gland has been lost in the history of the genera. If, on the other hand, the lack of a vitelline gland is a primitive character, the acquisition of uterine nutritive cells must still be a recent adaptation, as one would otherwise expect to meet such cells in other cestodes.

The uterine wall cells, after having given rise to the uterine nutritive cells, next supply the origin of the egg-pouches or paruterine organ.[1] In the first stages of the development of this organ we find parallel layers of plasma containing nuclei splitting off the terminal wall of the uterus (fig. 51). The

[1] It is a question which I cannot attempt to decide, whether the paruterine organ of Stilesia and Avitellina is homologous to the paruterine organ of other cestodes, as where it has been observed previously it has generally been held to arise outside the uterus. I am retaining the name as being convenient and as referring to a more or less well-known structure, but without prejudice as to its origin in other species. The paruterine organs of various cestodes may quite possibly be of different origin, and may only be convergent structures, as Fuhrmann has shown that they can arise independently in various unrelated genera.

nuclei are oblong, with two or three chromatin bodies, and resemble to some extent those of the uterine nutritive cells. The presence of the developing paruterine organ causes the wall of the uterus to bulge outwards at a very early stage. The portion thus pressed outwards is at first hemispherical, opening directly into the main body of the uterus, this portion might be termed the paruterine pouch (fig. 53). The next changes take place very quickly, and we find the mouth of the pouch contracting, the contraction being effected by muscles running around this portion of the uterus. As the contraction proceeds the pouch becomes more nearly globular, until it is finally almost spherical, remaining connected with the remainder of the uterus by a very narrow passage. These changes of their receptacle are not without their effect on the lamellæ, whose shape has to accommodate itself to the changes in form of the pouch; as they remain arranged parallel to the walls of the pouch they, too, become spherical; but the lamellæ are also growing quickly, and some of them force their way into the uterus as concentric hemispheres, whilst others form concentric hemispheres within the pouch. The lamellæ projecting into the uterus appear to grow very quickly, pressing the uterus and its eggs further and further away from the pouch; the uterus, which was at first merely a transverse tube, becomes globular through the invasion of the lamellæ, which have become almost spherical. Finally, as the lamellæ are still growing and as they have no more room to spread outwards, the only outlet remaining for them is by doubling back. Depressions appear on the surface of the lamellæ, deepen, pass through the neck into the pouch, carrying the eggs, which are already enclosed in their two envelopes and contain embryos, with them into the paruterine pouch. Finally, the lamellæ appear to complete the process of retroversion and return entirely through the neck of the pouch: none are left outside the pouch at all events. The growing back always takes place at several points at the same time, thus giving rise to more than one pocket; six or seven are usually formed (figs. 53–56, *pp.*).

The lamellæ are at first composed of a mass of plasma belonging to several nuclei and are fairly thick; with further development the thickness of the lamellæ becomes less and less, and they finally resemble thin fibrillæ on section. There can, however, be no doubt that the structure is lamellar and not fibrillar, as in whatever direction a section may pass through a paruterine organ, one always sees a concentric arrangement of "fibres" running within the plane of the section, but never by any chance sections through fibrillæ. As the lamellæ grow older the nuclei atrophy and finally disappear.

Directly anterior to the uteri lie pads of fibrous tissue (fig. 52), whose probable function is to give support to the paruterine organ, and perhaps also to act as cushions between the uteri and paruterine organs of adjacent segments. These pads take their origin from myoblasts, which are very frequent close in front of the uteri when the eggs are begining to enter that organ. The fibrous tissue, when fully developed, contains scattered nuclei, and its fibrillar structure is fairly apparent. It stains fairly vividly with eosin (fig. 48).

The cirrus and cirrus pouch arise out of a common anlage with the vagina, as already explained above. The dense mass of dark-staining nuclei, which gives rise to both, first splits into two masses; these become surrounded by myoblasts (fig. 44); then, in the middle of one of the two masses the vagina begins to develop, the cirrus and part of the vas deferens in the other. The epithelial cord arising in the middle of the cirrus pouch anlage is at a very early stage already convoluted, probably giving rise to the twisted portion of the vas deferens enclosed in the cirrus pouch

The vas deferens is, like the female ducts, formed of a solid cord of epithelial cells surrounded by a basal membrane (fig. 46); the hollow arises later. As in the female ducts, the epithelium finally atrophies entirely. Its lumen is then clothed with ciliæ.

The cirrus is straight, 34 μ long by 3 μ in diameter; it is devoid of hooks, bristles or cilia of any kind; it opens

directly into the vagina. I have never observed an intromission of the cirrus into the vagina. The cirrus muscles consist almost entirely of a circular muscle; the longitudinal muscle usually observed between the circular muscle and the cirrus appears to be wanting or extremely weak. Cirrus and vas deferens within the cirrus pouch are suspended by loose parenchym cells, which stretch themselves from the walls of the pouch, passing around and gripping the vas deferens. They act as a kind of mesentery in function (fig. 50).

The muscles of the cirrus pouch are very feeble. The whole cirrus apparatus gives one the impression that the cestode has lost the habit of cross-fertilisation, and that self-fertilisation has become the rule.

Conclusions.

(1) There is no subcuticula in the suckers.

(2) The cuticula can arise independently of the subcuticula.

(3) The subcuticular cells stand in direct connection with the dorsoventral and transverse muscles and form part of them.

(4) The parenchyma muscles are produced by three kinds of myoblasts: (*a*) Bipolar myoblasts with terminal fibrillæ; (*b*) bipolar myoblasts with lateral fibrilla; (*c*) elongate bipolar myoblasts lying axially in the tubiform muscles of the longitudinal muscle.

(5) The dorsal canals are surrounded by nephrocytes, which are homologous with the parent cells of the flame-cells.

(6) There are ganglion cells in the suckers, connected by neurofibrillæ with the "Sommer-Landois" cells of the subcuticular muscles of the sucker.

(7) In addition to oöcytes, nutritive cells are produced in the ovaries.

(8) The oöcytes mature before leaving the ovarium.

(9) The oöcytes arrive fertilised in the uterus.

(10) The oöcytes in the uterus are surrounded by nutritive cells of uterine origin.

(11) The paruterine organ is contained in a pouch of the uterus, and arises within the uterus; its structure is lamellar.

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EXPLANATION OF PLATES 12–14,

Illustrating Mr. Lewis Henry Gough's "Monograph of the Tape-worms of the Sub-family Avitellininæ, being a Revision of the Genus Stilesia, and an Account of the Histology of Avitellina centripunctata (Riv.)."

PLATE 12.

Avitellina centripunctata (Rivolta).

Fig. 1.—Portion of three segments at male sexual ripeness. × 99.

Fig. 2.—Oncosphære. × 588.

Fig. 3.—Four segments with fully developed paruterine organs. × 99.

Fig. 4.—Cirrus-pouch and vagina. × 380.

Fig. 5.—Left half of the excretory canals of scolex, lateral view.

Fig. 6.—Right half of the excretory canals, lateral view.

Fig. 7.—Scolex.

Stilesia vittata, Railliet.

Fig. 8.—Pore-side of a segment at male sexual ripeness. × 99.

Fig. 9.—Oncosphære. × 588.

Stilesia globipunctata (Rivolta).

Fig. 10.—Pore-side of a segment at male sexual ripeness. × 99.

Fig. 11.—Oncosphære. × 588.

Fig. 12.—Scolex.

Stilesia hepatica, Wolffhügel.

Fig. 13.—Pore-side of a segment at male sexual ripeness. × 99.

Fig. 14.—Segment with developing paruterine organs. × 99.

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Fig. 16.—Cirrus pouch and vagina. × 380.

PLATE 13.

Avitellina centripunctata (Rivolta).

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Fig. 18.—Cuticula of the proglottids, silver nitrate fixation. × 784.

Fig. 19.—Subcuticula and cuticula. × 784.

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Tænia serrata, Rud.

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Avitellina centripunctata (Rivolta).

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PLATE 14.

Avitellina centripunctata (Rivolta).

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Fig. 49.—Portion of uterus, with oöcytes surrounded by nutritive cells. × 1176.

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Fig. 56.—Fully developed paruterine organ; all the eggs have entered the pockets of the pouch.

Figs. 57–65.—Oöcytes in various stages.

List of Abbreviations used.

[The abbreviations used are the same throughout the paper.]

a. Sucker. *at.* Cloaca. *b. m.* Basal membrane. *b. p.* Basal plate. *c.* Cirrus. *c. c.* Connecting canal. *ch.* Chromatin. *c. l.* Comidial layer. *c. p.* Cirrus pouch. *c. s.* Canalis seminalis. *cu.* Cuticula. *d.* Dividing nucleus. *d. c.* Dorsal canal. *e.* Egg. *ep.* Epithelium. *ep. c.* Epithelial cell. *f.* Fibrilla. *f. c.* Flame-cell. *f. c. d.* Developing flame-cell. *fl.* Flame. *f. p.* Fibrous pad. *fu.* Funnel. *g.* Gland-cells surrounding the vagina. *gl.* Glia-cells. *h. l.* Homogeneous layer. *i. d.* Interuterine duct. *k.* Capillary. *k. c.* Capillary cell. *l.* Lumen. *l. i.* Inner layer. *l. o.* Outer layer. *m.* Muscle. *mb.* Myoblast. *m. f.* Muscle-fibrilla. *n.* Nerve. *n. c.* Nutritive cell. *nf.* Neurofibrilla.

nl. Nucleolus. *nn.* Nucleus. *o.* Ovarium. *od.* Oviduct. *p.* Paruterine organ. *par.* "Parenchyma" cell, suspensory cell in the cirrus pouch. *pou.* Paruterine pouch. *r.* Nephrocyte. *r. f.* Radial fibres. *r. s.* Receptaculum seminis. *s.* Spermatozoon. *s. c.* Subcuticular cell. *s. l.* "Sommer-Landois" cell. *s. m.* Subcuticular muscle. *t.* Testicle. *t. b.* Tigroid bodies. *t. c.* Transverse canal. *u.* Uterus. *u. d.* Uterine duct. *v.* Vagina. *v. c.* Ventral canal. *v. d.* Vas deferens. *v. s.* Vesicula seminalis. *x.* Corpuscle. *y.* Centrosome. *z.* Fusing sperma and egg nucleus